CONFRONTATION BEHAVIOR BETWEEN *SOLENOPSIS INVICTA* BUREN AND CERTAIN ANT SPECIES NATIVE TO FLORIDA

By

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To my grandmother and parents.

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TABLE OF CONTENTS

	Page
ACKNOWLEDGEMENTS	iii
LIST OF TABLES	vii
LIST OF FIGURES	ix
ABSTRACT	xi
INTRODUCTION	1
REVIEW OF LITERATURE	4
Definitions	4
Chemical basis of alarm-attack behavior	4
Interspecific competition in ants	6
Patterns of alarm-defense behavior in ants	10
MATERIALS AND METHODS	12
Location of study	12
Collection and rearing of ants	12
Underground nest structures	15
Confrontation behavior	15
Analysis of confrontation behavior	16
Confrontation index	17
CONFRONTATION STUDIES	18
Species studied	18
RESULTS OF CONFRONTATIONS	23
SUBFAMILY PONERINAE	23
Hypoponera opacicepa (Mayr)	23
Leptogenys minax Wheeler	28
Odontomachus ruginodis Wheeler	31
SUBFAMILY DORYLINAE	41
Neivamyrmex opacithorax (Emery)	41
SUBFAMILY MYRMICINAE	45
Aphaenogaster texana carolinensis Wheeler	45
Aphaenogaster tennesseensis Wheeler	48
Aphaenogaster ashmeadi Emery	52
Pheidole dentata Mayr	55
Pheidole morrisi Forel	60

Page

Solenopsis geminata (Fabricius) 64
Solenopsis pergandei Forel 73
Pogonomyrmex badius (Latreille) 75
Cyphomyrmex rimosus minutus Mayr 79
Trachymyrmex septentrionalis (McCook) 84
Crematogaster atkinsoni Wheeler 89
Crematogaster atkinsoni Mayr 93
Crematogaster minutissima Mayr 96
SUBFAMILY PSEUDOMYRMECINAE 98
Pseudomyrmex pallidus F. Smith 98
Pseudomyrmex brunneus F. Smith 106
SUBFAMILY DOLICHODERINAE 111
Iridomyrmex pruinosus (Roger) 111
Conomyrma flavopecta (M. Smith) 113
Conomyrma insana (Buckley) 115
SUBFAMILY FORMICINAE 120
Lasius neoniger Emery 120
Paratrechina sp. 124
Formica schaufussi dolosa Wheeler 127
Camponotus impressus (Roger) 132
Camponotus abdominalis floridanus (Buckley) 137

CONFRONTATION INDEX 142

DISCUSSION AND CONCLUSIONS 150

APPENDIX 1 160

APPENDIX 2 164

APPENDIX 3 165

APPENDIX 4 166

APPENDIX 5 167

APPENDIX 6 168

APPENDIX 7 169

APPENDIX 8 172

LITERATURE CITED 173

BIOGRAPHICAL SKETCH 181

LIST OF TABLES

Table		Page
1.	Mean number of mandibular closures shown by *Odontomachus ruginodis* Wheeler to imported fire ant workers and dental stick	37
2	Attack responses shown by *Pheidole dentata* majors and minors towards *Solenopsis invicta* workers during 20 min of confrontation	58
3	Attack responses shown by *Pheidole morrisi* majors and minors towards *Solenopsis invicta* workers during 20 min of confrontation	62
4.	Frequency of mandibular attacks exhibited by *Solenopsis invicta* workers towards *S. geminata* workers within 5 min of confrontation	67
5.	Relation of mechanical stimulation (teasing with forceps) of different sensory areas on the persistance of aggression-suppression-akinesis (ASA) response in *Cyphomyrmex rimosus minutus*	81
6.	Relation of disturbance by the *Solenopsis invicta* workers to the persistence of ASA response in *Cyphomyrmex rimosus minutus* workers	83
7.	Confrontation responses shown by *Trachymyrmex septentrionalis* and *Solenopsis invicta* during 1 hr of observation	88
8	Frequency of attack responses shown towards *Solenopsis invicta* by *Crematogaster atkinsoni* and *C. ashmeadi* during 20 min exposure	91
9	Time interval (in sec) between contact chemoreception and nest invasion between *Solenopsis invicta*, *Pseudomyrmex pallidus* and *P. brunneus*	102
10	Time lapse (in min) between "alert" to "attack" responses of the red imported fire ant in *Pseudomyrmex pallidus* and *Pseudomyrmex brunneus*	103
11.	Frequency of two or more cumulative responses occurring within first 20 min of confrontation between *Pseudomyrmex pallidus* and *Solenopsis invicta*	105

Table | Page

12. Frequency of two or more cumulative responses occurring within first 20 min of confrontation between *Pseudomyrmex brunneus* and *Solenopsis invicta* 109

13. Frequency of aggressive responses shown by *Pseudomyrmex pallidus* and *P. brunneus* to *Solenopsis invicta* within first 20 min of confrontation 110

14. Frequency of attack responses shown by *Formica schaufussi dolosa* towards *Solenopsis invicta* during 20 min of confrontation 130

15. Frequency of attack responses shown by *Solenopsis invicta* towards *Formica schaufussi dolosa* during 20 min of confrontation 131

16. Defensive responses shown by *Camponotus impressus* workers during confrontation with *Solenopsis invicta* 138

17. Results of the confrontation between *Solenopsis invicta* and common terrestrial ant species (24 hr confrontation at 27°C) 145

LIST OF FIGURES

Figure		Page
1.	A. Apparatus for Confrontation Index studies. B. Apparatus for confrontation studies between *Solenopsis invicta* and tarricolous, or C arboricolous ant species. D Q-Tips insertions for glass tube nests	13
2.	Map of Tall Timbers Research Station area	22
3.	Aggression-suppression-akinesis (ASA) responses elicited by *Hypoponera opaciceps* (1), *Trachymyrmex septentrionalis* (2), and *Cyphomyrmex rimosus minutus* (3), and frontal view of *T. septentrionalis* (Ts) and *C. rimosus minutus* (Cr) showing well developed antennal scrobes	25
4.	Confrontation behavior between *Odontomachus ruginodis* and *Solenopsis invicta* workers	34
5.	Profile of *Odontomachus ruginodis* with open mandibles (top), and cuticular asperities at the base of the 2nd gastric tergite of *O. ruginodis* (bottom)	40
6.	Gaster-flexing posture exhibited by a *Solenopsis invicta* worker in the presence of *S. geminata* workers (top), Two *S. invicta* miners salzing the appendages of a *S. geminata* major, and stinging its head and gaster (bottom, left), Two *S. invicta* miners salzing the antenna and mandible of a *S. geminata* major and stinging its alltrunk (bottom, right).	69
7.	Comparison of the nest building tendency of *S. invicta* and *S. geminata* in a vertical plane	71
8.	Expulsion behavior in arboricolous species. 1. *Camponotus (Colobopsis) impressus* (C) expelling a nest-invading *S. invicta* worker, 2. *Pseudomyrmex pallidus* (Pp) expelling a nest-invading *S. invicta* worker	101
9.	Nest structures of *Conomyrma flavopecta* (Cf) and *Conomyrma insana* (Ci)	117
10.	A *Lasius neoniger* worker grasping the flagellar portion of *S. invicta* antenna between its mandibles and clypeus, pulling it through while allowing slack	123

Figure Page

11. 1. Cork-shaped head adapted in the major worker of *Camponotus impressus* for phragmosis 2. Head of the minor worker of the same 3. Handlebar sensilla of the phragmatic surface 135

12. Confrontation indices of native ant species 148

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The red imported fire ant, *Solenopsis invicta* Buren, was confronted with 27 terrestrial and arboreal ant species common to Florida ecosystems. Laboratory studies were conducted under simulated natural nesting conditions at 27 ± 2°C temperature. Field observations at the Tall Timbers Research Station, Tallahassee, Florida, conducted from 1969 to 1972, supplemented the laboratory observations.

Defensive potential of the terrestrial ant species, denoted as "confrontation index," was calculated as a constant by exposing equal numbers of the confronting species and then increasing the number of the subdued species. Defensive potential of one ponerine species, *Odontomachus ruginodis* Wheeler, three species of *Aphaenogaster* and two species of Formicinae, *Lasius neoniger* Emery and *Paratrechina* sp., exceeded that of the red imported fire ant under captive conditions. These species either possessed specialized defense adaptations such as scissor-like mandibles, or stung or paralyzed the attacking workers with their mandibular and acidopore secretions. In nature, the population density of the above species exceeded that of the red imported fire ant only under localized conditions. The *S. invicta* venom was a potent toxicant to all the species studied.

A majority of species exhibited passive defensiveness momentarily or for several minutes prior to escape. Attine species, *Cyphomyrmex rimosus minutus* and *Trachymyrmex septentrionalis*, coexisted with *S. invicta* and foraged on its dead. Their crush-resistant cuticle, along with akinesis and egression suppressing were to their advantage. A dolichoderine species, *Conomyrma flavopecta* (M.R. Smith), nested beside the fire ant mounds and its potent repellent secretions were to its advantage due to its necrophagy of the fire ant. *Conomyrma insana* (Buckley) defended itself whenever it was abundant since its trophic level was the same as the red imported fire ant.

Behavioral analysis of *S. invicta* and closely related oligomorphic and polymorphic species disclosed more active defensive interactions by major workers than by minors in *Pheidole* spp., and vice versa in *Solenopsis geminata* (Fabricius) and *Pogonomyrmex barbus* (Latreille). The guard ants of arboreal species exhibited defensive frenzy prior to their nest invasion by *S. invicta*. Escape behavior and subsequent swarming were pronounced in the species of *Pheidole*, *Aphaenogaster*, *Formica*, *Crematogaster* and *Camponotus*. Epigeic, hypogaeic and arboreal nesting species protected their colonies through their specialized nest structures.

Interspecific competition was regarded as a major factor regulating stability among ant populations. Equilibrium colony densities among species at a similar trophic level is conjectured, especially during their steady competition for nesting sites and honeydew-producing fauna. The rapid spread of the red imported fire ant throughout the southeastern United States indicates no such equilibrium at the present time among it and the native species. It may also suggest greater effects of inter-

specific competition on the spatial organization in ants than ground predation of the workers, brood, nuptial masses and social parasitization where the effects are more localized.

INTRODUCTION

The red imported fire ant, *Solenopsis invicta* Buren, has caused considerable controversy since its discovery in this country almost 28 years ago. In most instances, it is considered as a nuisance species. It has been noted as a pest of agricultural crops (Wilson 1959), livestock (Lyle and Fortune 1948, Eden and Arant 1949, USDA report 1958, Wilson 1958a), wildlife (Johnson 1961, Hill 1962), and was even found to poison fish (Lee 1960). It has been observed tending scales and aphids (Wilson 1958a, Nielsson et al. 1974, R. C. Wilkinson, personal communication). At the same time, George (1958), Arant et al. (1958), and Baker (1958), were skeptical of its damage to the wildlife. According to Hays (1958), Green (1967), and Wilson and Oliver (1969), its diet is largely made up of insects. Apparently, in some instances, it is a beneficial predator though its importance has often been overlooked (Long et al. 1958, Newsom et al. 1959, Negom and Hensley 1967, Hensley 1971).

Apart from the controversial status of this species, it is a remarkably versatile ant (Wilson 1959), and "one of the most successful insects ever to invade the USA" (Buren 1972). There has been a growing concern about the necrotoxic (Caro et al. 1957), hemolytic (Adrouny et al. 1959), and medical properties of its venom. Moreover, the species-displacing ability of the red imported fire ant (Wilson and Brown 1958), and its explosive rate of spread over the southeastern U.S., as far west as Texas, pose an ecological threat.

Auguste Forel (1928) stated that, "The greatest enemies of ants are other ants, just as the greatest enemies of men are other men." E. O. Wilson (1971) ascertained that the worst enemies of social insects are other social insects. Documentation of the fierce competition for nest sites, food and territory in ants has been used to explain general competition theory in biology by Wilson (1971), Orlan (1955, 1965) and many others. However, so far, there have been very few attempts to correlate population interactions (exploitation, interference, and competition, Pontin 1961) and individual behavior in ant species. Pontin (1961, 1963), and Wilson (1971) speculated that with our knowledge of exacting contest-competition among and within the ant species, it will be possible to analyze individual behavior in terms of population densities.

According to Wilson (1971), overt forms of aggressive behavior in ants have been in the following circumstances: (1) where the species have been recently introduced and are new to the competitors in the new area of introduction; (2) where the species are strongly territorial; (3) where the habitats have been artificially simplified, as in cultivated land and urban environments so that species brought into juxtaposition are ones which seldom encounter each other in their more complex environments. Many epigaeic species of *Eciton* attack many species of ants and prey on their brood (Schnairia 1957, Rettenmeyer 1963), so do the African army ants. The "sanguinary ants" (*Formica sanguinea* group) are very aggressive and territorial. They attack their slave species such as *F. fusca* or *F. rufibarbis* and snatch away their brood (Wheeler 1913). According to W. H. Whitcomb and R. Williams (personal communication) such aggression also occurs both in tropical and temperate regions where sudden ecological changes give unusual advantage to a particular species.

Solenopsis invicta Buren follows Wilson's criteria described above, and has been a potential aggressive ant towards the American species. The present study is an attempt to document the confrontation behavior of the red imported fire ant towards common arboreal and terrestrial ants found in Florida. We need to understand the inter- and intra-specific competition between the red imported fire ant and other species, both in the field and in the laboratory. Precise laboratory observations should reveal not only the attempts of frontal assaults but also the otherwise latent attempts in the absence of direct physical encounters. The behavioral patterns presumably can be related to future field observations.

An opportunity was presented to carry out this investigation at Tall Timbers Research Station in North Florida. The Tall Timbers area has been an excellent locus, devoid of insecticidal application for at least 80 years. Microhabitats of its ecological components are endowed with rich ant fauna. There was ample space for field and laboratory observations.

Varied defense mechanisms, akinesis, appeasement, repellance, attraction and direct attacks, were evaluated in terms of survival of Florida ant species in the presence of the red imported fire ant. Whenever relevant, attempts were made to study the micromorphology of the structures involved in defense and escape. The comparison of aggressive behavior between the ant species necessitated a "confrontation index" specific for each ant species.

This study should aid our understanding of aggression and contest-competition type interactions among ant species. Hopefully, this study will be useful in the efforts directed to manage the red imported fire ant populations.

REVIEW OF LITERATURE

Definitions

Interspecific competition in ants has been defined by Pontin (1961, 1963) as an interaction which lowers the densities of the competing species compared with the density each would reach alone. Robertson (1971) discussed the complications in using certain behavioral terms such as "attack," "offense," "defense," "attraction," "repellence," etc., in studying the components of behavioral patterns in *Myrmecia gulosa*. Recently, Shorey (1973) pointed out the broad usage of the term "alarm" throughout ant literature. Lorenz's definition (1966) of aggression (unprovoked attacks motivated by anger, and not by hunger), cannot be validated for insects since unprovoked attacks on the prey are indistinct from those motivated to subjugate an individual of the same or the other species. It has been demonstrated that the pattern of behavior in ant species is the same although its components differ in emphasis whether the attack is launched by a solitary forager or by a group of workers defending the nest territory (Wallis 1962, Robertson 1971).

Chemical basis of alarm-attack behavior

In a study of the ant subfamilies Myrmicinae and Formicinae, the members of which are highly organized socially, Ayre (1968) found that attacks on the enemies stimulated the release of pheromones which intensified further attacks. The reaction is sometimes restricted to high concentrations of pheromones (Wilson 1965) within the nest, on the trail, or to feeding places (Maschwitz 1964). According to Robertson (1971),

In the primitive generalized Australian subfamily Myrmeciinae, there is a more complex pattern of aggressive behavior than in advanced Formicidae.

Alarm and attack are two major aspects of aggressive behavior. Alarm has been extensively studied in Formicinae (Regnier and Wilson 1968, 1969, Maschwitz 1964, Wilson 1965), Dolichoderine (Wilson and Pavan 1959, Blum et al. 1966, McGurk et al. 1968), and Myrmicinae (Wilson 1958b, Bossert and Wilson 1963, McGurk et al. 1966, Crewe et al. 1970, Blum et al. 1969). In the subfamilies Dorylinae, Myrmicinae and Formicinae, alarm behavior is associated with manifestations of attraction and attack. In all cases, behavior is social and evoked in the field to protect nest territory (Wilson 1958b, Brown 1959, Maschwitz 1966, Ayre 1968).

Dufour's gland has been known to produce alarm pheromones in the Formicinae (*Lasius fuliginosus* and *Formica polyctena*, Maschwitz 1964), and an odor trail pheromone in Myrmicinae (*Solenopsis saevissima richteri*, Wilson 1962). Odor trail pheromones are secreted from the rectal area of Ponerinae (Wilson 1965), Dorylinae (Blum and Portocarrero 1964), and Formicinae (Carthy 1951, Blum and Wilson 1964). However, Robertson (1971) observed alarm pheromones from the DuFour's gland of Myrmicinae and some attack reaction from the rectal secretion.

Alarm reaction is also produced by the mandibular exocrine glands in a wide range of species belonging to Ponerinae, Dorylinae, Myrmicinae and Formicinae (Wilson 1965). In *Myrmecia gulosa* (Myrmeciinae) the mandibular glands produce an attack pheromone which is distinct from an alarm pheromone (Robertson 1971). Aggressive behavior also occurs in sting-bearing subfamilies such as Dorylinae, Pseudomyrmicinae, and Myrmicinae, but in Formicinae, most forms use the contents of their venom reservoirs as defensive sprays though some behave aggressively. In Dolichoderinae,

the aggression control glands are vestigial and are replaced by glands whose function is defensive (Wilson 1965, Blum et al. 1966, Wilson 1971, Robertson 1971).

Interspecific competition in ants

There is a widely defined segregation in ants due to structural specificity, stratified foraging zones, and nesting zones. An alternative way of segregation is specialized offensive skills. Usually one species dominates an area while the others extend to less hostile but equally productive parts in the ecosystem (Brian 1965). Stebayev (1971), during his work on competition among the ground inhabiting species, showed that the nests of dominant species are the spatial organization centers for other species that concentrically nest around it and increase their foraging territories radially when the dominant species ceases foraging. Some species, such as *Formica sanguinea* (Latr.) and F. *rufa* (Lin.), live a dual mode of life to exploit the habitat. They form (1) solitary colonies that subdue other species, and (2) smaller, less hostile colonies that contract into fewer larger ones in winter (Markovsky 1963). Wilson et al. (1971) observed seasonal changes in the territorial boundaries of S. *xerophilum* (probably S. *smithi*). The smaller colonies had smaller territories than the larger ones. They observed the dominance of stronger colonies and after confrontation between the workers of adjacent colonies - their reduction to an extent of 15-40 per acre, a larger number of initial small colonies were destroyed. This species was seen to defend against other ant species at the same trophic level.

The world-wide dispersal of such pest species as *Pheidole megacephala* and *Tapinoma humile* has been enhanced by versatile feeding habits, pleometrosis and seminomadic behavior and movement by commerce. They are

well equipped for offense and compete successfully with the native species (Goetsch 1951, Haskins 1945, Elton 1958).

The species displacement phenomenon in *S. saevissima* (probably *S. invicta*) has been discussed by Wilson and Brown (1958). Wilson described two color variants of *Solenopsis saevissima richteri*, explainable on the basis of multiple pleiotrophic alleles. The dark form, which was known to have been in the Bayfront area of Mobile, Alabama since 1918 (Creighton 1930), was dominated by a light or red form (a possible second introduction, or a favorable mutation within the population) which tended to be hypervigorous and intensely antagonistic towards the dark form (Wilson 1951). Recently, Buren (1972) championed a new taxonomic model for *saevissima* complex and delimited the dark form (now found in northern Mississippi) as *S. richteri* Forel, and the light or red form *S. invicta* Buren, a new species. He concluded that disappearance of *richteri* from the Mobile area was due to displacement by *invicta* and not by genetic swamping.

Vanderplank (1960) found that numerically superior *Anoplolepis custodiens* enabled it to replace *A. longipes* and *Oecophylla longinoda*; *Pheidole punctulata* replaced *O. longinoda* in dry weather, while the reverse was true during wet weather. In Brown's (1959) study, the success of either *Iridomyrmex* or *Oecophylla* depended on number of the species adapted to that situation. Wilson and Brown (1958) found that the success of the red form of *Solenopsis saevissima richteri* (apparently *S. invicta*) depended on the red form's superior ability to find and destroy the young queens and colonies of the dark form.

According to Brian (1965), competition between taxonomically close species is fierce when they confront. However, there are many ways to

reduce these interactions where major structural, physiological, trophic and organizational differences occur. Wilson and Brown (1958) reported that the spread of the imported fire ant has a profound influence on the native ant species within its range. *Solenopsis xyloni* has been eliminated where *S. saevissima richteri* is dominant since both the species have similar ecological preferences. Another species, *S. geminata*, has been reduced both in ecological range and genetic variability due to the competitive pressure from *S. saevissima richteri*. Its sympatric populations are confined to woodlands wherever *saevissima* appears to compete less successfully. Whitcomb et al. (1972) have similar observations on *S. invicta* from Florida soybean fields.

The Argentine ant, *Iridomyrmex humilis* Mayr, eliminated many native ants in the Mobile area until 1920 (Creighton 1950), and may have pushed the dark form of *S. saevissima* northward initially. It is now limited to urban areas due to the invasion of *S. saevissima* (apparently *S. invicta*) which occupied various habitats (Wilson and Eads 1949), the exact basis of segregation is not known (Wilson 1951). Colonial forms of *Formica fusca* and *F. polyctena* spread in Siberian forests destroying and displacing other species (Markovsky 1963). Brian (1965) observed that in England, *Myrmica scabrinodis*, *M. ruginodis*, *Formica lemani*, and *Leptothorax acervorum* showed aggregated nest distribution until the nesting sites were sparse. After that, *F. lemani* drove many others off, forming specific zones of distribution. *L. acervorum* escaped competition by boring fine galleries and changing food gathering time (Elton and Miller 1954). While studying the ants of Mt. Hakkoda, Yasuno (1963, 1964) found that *Formica fusca* restricted *Myrmica rugineodis* to woodlands. He stressed the correlation of worker size to coexistence in ant species.

Golley and Gentry (1964) pointed out that in the old field ecosystem, large *Pogonomyrmex badius* and small *Dorymyrmex* sp. occur together. Brian and Brian (1955) noted that two subspecies of *Myrmica rubra* (L.) coexisted due to ecodifferentiation, but *microgyna* prevented intrusion of *macrogyna* when both confronted. Markovsky (1962) speculated that in evolutionary sense dominant ants of the *Formica rufa* group forced the smaller species like *Lasius niger* and *Myrmica rubra* to live underground. However, *L. niger* tended nest aphids (Way 1954) and may have resorted to such nesting. Way (1954) recorded that *Cecophylla* left small colonies of small ants on tree trunks while it cleared others off the trees. The army ant, *Eciton hamatum* (Fabr.) was not hostile to smaller ants and shared the trails of *Atta* (Rettenmeyer 1963). When smaller ants (*Solenopsis* spp) nested in the nests of the larger ones, they shared their galleries and food (Wheeler 1910).

In a slave-raiding species, less hostility is shown to the workers of the slave species. When food was limited the slave ants are however, eaten together with other ants by *Formica sanguinea* (Markovsky 1963). The species of nomadic army ants such as *Eciton* spp. in Neotropics (Rettenmeyer 1963), and *Dorylus wilverthi* and *D. nigricans* in Africa often coexisted because of the difference in their food habits (Schneirla 1957). Attine ants are characteristically non-aggressive and several species may live together without interference (Weber 1972). Wilson (1951) found Mobile and Baldwin counties (Alabama) co-occupied by *S. xyloni richteri* (probably *S. invicta*) and another introduced species, *Brachymyrmex heeri obscurior* Forel. Wilson et al. (1971) and earlier workers reported what appears to be *Conomyrma flavopecta* M. R. Smith nesting at the very edge of the red imported fire ant mound and in the latter's foraging territory.

Patterns of alarm-defense behavior in ants

Göetsch (1953) accounted for the patterns of aggressive behavior in many ant species. He suggested that the spread of *Iridomyrmex humilis* was due to its competition with other species. Wallis (1962) studied the factors eliciting and influencing aggressive behavior in *Formica fusca*. He regarded threat, dragging, and seizing as high intensity aggressive responses. The responses of *Formica fusca* differed towards alien species from those towards nest-mates. Increased temperature and hunger increased aggressive responses. However, odor of the colony was a potent stimulus to aggression.

Coyle (1966) described three components of defensive behavior in the tribe Cephalotini species of *Panurgyrocerus*: (1) vertical positioning of gaster, (2) minimum movement, and (3) release of defensive secretion from the apex of the gaster.

Robertson (1971) described two more aspects of primary alarm response, alert and activation. She defined alarm and attack as the primary aggressive responses in the primitive Myrmecinae. Wilson (1971) reviewed the subject of alarm communication in ants. According to him, the chemical elements of alarm signals fade quickly and there is no positive feedback for the stimulus to be continuous. Chemical bases of alarm behavior are reviewed by Blum (1969) and Shorey (1973), and those of defensive behavior are reviewed by Roth and Eisner (1962).

Large-eyed ants detect moving objects (Jander 1957, Ayre 1963, Voss 1967) and activate other workers for attacking a moving prey (Stager 1931 in Wilson 1971). Wilson (1962, 1971) considered the "Stager effect" among workers as an elementary form of visual communication.

The most elaborate form of recruitment communication in ants is the

odor trail system. It evolved, at least in some groups, from tandem running (Wilson 1971). Trail pheromones tend to be species specific, they are specific to a group of species within genera (Wilson and Pavan 1959, Blum 1966). Watkins (1964) found no pheromone differences in *Neivamyrmex* spp. Wilson (1962) found the trails of *Solenopsis saevissima* (probably *S. invicta*) attractive to *S. xyloni* but not to *S. geminata*. *S. geminata* trails were not attractive to either. No trail substances in ants are chemically defined.

Wheeler (1903) and Janet (1893) considered stridulation as an important means of communication in ants. Haskins and Enzmann (1938) showed that leafcutting ants were deaf to air-borne sound but sensitive to soil-borne vibrations, and even such vibrations due to stridulation. However, ordinary mechanical stimuli and stridulation were considered to play a minor role in alarm signals by Wilson (1971). Not much is known about the antennal language; most antennation is believed to serve in receiving the chemical information such as recognition odor, rather than in sending it (Wilson 1971)

MATERIALS AND METHODS

Location of study

The ants were on the property of the Tall Timbers Research Station in North Florida, situated at 30.7° North latitude along the Northern shore of Lake Iamonia (Fig. 2). The 2,800 acre area consists of such widely different ecosystems as mesophyllic hammocks, fire-controlled, monotypic pine woods; cultivated and fallow fields; lawns, and lake-shore vegetation. Year-round comparatively high humidity is congenial for the flora and fauna. Studies on the behavior analysis were also conducted at the University of Florida and the USDA Attractants and Behavior Laboratory in Gainesville, Florida. A large reconstructed barn on the station property served as a field laboratory for many of the confrontation investigations.

Collection and rearing of ants

Arboreal ants were collected by breaking and cutting open twigs of several soft-pithy plants, shrubs, and trees such as button bush (*Cephalanthus occidentalis* L.), pines (*Pinus* spp.), magnolia (*Magnolia* spp.), mulberry (*Morus* sp.), catalpa (*Catalpa speciosa*), and many vines such as *Smilax* spp., wild grape (*Vitis* spp.), blackberry (*Rubus* sp.), sumac (*Rhus glabra* L.), and *Eupatorium* spp. Culms of bamboo and some perennial grasses also provided nesting sites to some species. Year-round collections were made and the ants were reared in the laboratory at 27±3°C. Most arboreal ants nested successfully in glass tubing 30 cm in length and 0.4 cm inner diameter. The tubes were held vertically by casting liquid

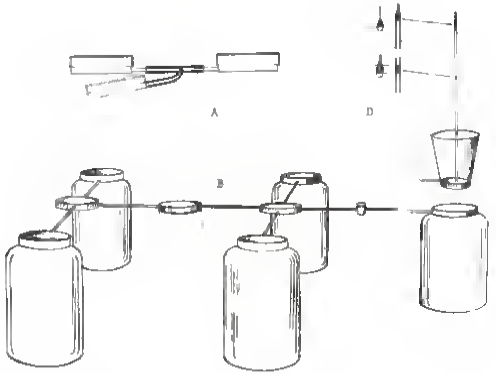


Figure 1. A. Apparatus for Confrontation Index studies. B. Apparatus for confrontation studies between S. invicta and terricolous, or C. arboricolous ant species. D. Q Tips insertions for glass tube nests.

plastic (Castolite, Cope Plastics Inc., Godfrey, Ill.) around them in 12 fluid oz. plastic tumblers (Plasses, Plastics Inc., St. Paul, Minn.). To simulate natural nests the glass tubes were compartmented by 1/2 cm endpieces of hollow Q-tip holders (Johnson and Johnson, New Brunswick, N. J.), inserted 6 cm apart. The upper end of each tube was narrowed to a passageway slightly larger than the ant's thorax or abdomen by plugging it with a 2.5 cm piece of Q-tip holder (Fig. 1, D). The ants from the twigs were dropped into the tumbler. They occupied the simulated nest within 24 hr. The ants were given access to water through a 5.5 cm piece of Q-tip holder passed up to the bottom of a snap-cap vial through its cap. The vial was filled with tap water or 5% honey solution.

Terrestrial ants were collected by digging around their nest or mound, well encompassing the colony. The nests were vertically sliced from one side (mostly the sunward side) and the brood cells were exposed. The brood was collected with an aspirator and held in gallon jars. Separate gallon jars or aquarium jars were half filled with nesting soil and the ants were allowed to nest. If a species required two or more gallon jars, they were connected with a 0.4 cm inner diameter, 30 cm glass tubing via a petri dish (Fig. 1). The petri dish held food and water.

The ants were confined to the containers by rimming the containers' inner edges with talcum powder or heavy mineral oil. Both the substances served to reduce friction between the ants' tarsal grips and the container surface, thus reducing their crawling capacity.

Ants nesting in rotting wood were reared in the laboratory by holding the pieces of their nesting wood in the gallon jars.

Soil-free ant colonies were raised in 20 cm diameter, 3 cm high circular plastic cells (inner diameter 18 cm and height 1 cm). Other specifications

of the cells were identical to the ones described by Wilson (1962). The cells will be referred to as "Wilson cells" henceforth.

Laboratory colonies were fed on agar-based semisynthetic diets (Bhatkar and Whitcomb 1970). The ants fed on the diet when it was semi-solid or jelly-dry. The diet was supplemented with live insect tissue whenever required.

Underground nest structures:

The tunneling behavior of the terrestrial ants was studied by using nests similar to commercially available vertical ant nests (Wards Catalog #701, 1970-71). The nests were 38 cm x 30 cm plastic rectangles with 0.7 cm thickness and provided 34.5 cm x 29 cm x 0.15 cm nesting space.

Confrontation behavior:

a. Terrestrial species: A centrally partitioned large plastic nest (40 cm x 30 cm x 0.6 cm) was used to observe confrontation effect on the nest architecture of two dissimilar species. The species were allowed to nest on two sides of the partition, and an apical 4 cm piece of the partition was removed; the nest was otherwise sealed. It could be connected through glass tubing to the Wilson cells where the soil-free colonies were raised. The ants excavated soil in preference to soil-free condition.

The colonies raised in gallon jars or aquarium jars were connected through a 0.4 cm diameter, 20 cm glass tubing (confrontation tubing), via the feeding dish (Fig. 1, 9). Soil-free colonies of dissimilar species reared in Wilson cells were also similarly connected through a two-way stopcock. A 24-48 hr time lapse was given for habituation prior to opening the passage between colonies.

b. Arboreal species: The natural nests in hollow twigs and the

artificial glass nests were connected through a 0.4 cm diameter, 20 cm glass tubing to the *S. invicta* colonies raised in Wilson cells or glass jars (Fig. 1, C).

Temperature (27±1°C) and Rh (70%) were held constant during all the confrontation experiments.

c. Individual defense mechanisms: Defensive functions of certain ant parts such as mandibles, sting, etc., were studied by holding live ants in slits made in paper strips. Three pin holes were 1 cm apart and 1 cm from the outer edge in a 5 cm x 2 cm strip of paper. The ant could be passed along its cervix or postpetiole through the open slit and slid up to the pin hole. The slit edges were brought back to normal position and taped securing the ends. The paper could now be rolled into a tube exposing either the head or abdomen and the ends of the roll taped to avoid any ants attacking unexposed portions. The tube was held in a petri dish containing alien species.

For short-duration marking of individual ants, acrylic polymer emulsion color (Newere, Ideal Brushes, Inc., North Hollywood, Calif.) was used. The thoracic and postpetiolar regions could be successfully marked for over two weeks.

Analysis of confrontation behavior:

The imported fire ant (*Solenopsis invicta* Buren) was considered as a reference species. Its aggressive responses towards native species, and protective and defensive responses of it and the native species were critically studied. The behavior of the confronting species was analyzed by listening to tape recorded notes, by 35 mm still photography, by 8 and 16 mm cinematography, and wherever possible, by scanning sensory morphology with the use of Cambridge Mark II Stereoscan Electron Microscope. Sketches

were made from a series of photographs depicting the elements of behavior. The laboratory observations were supplemented by field observations.

Confrontation Index

A simple numerical index (confrontation index) was calculated in relation to the red imported fire ant. An exact number of the red imported fire ant was confined to 9 cm x 2.5 cm petri dish which was connected to another identical petri dish containing the same number, or its simple multiple, of another species. Connecting the petri dishes through 5 cm pieces of 0.4 cm diameter glass tubes and an interconnecting 5 cm piece of rubber tubing made it possible to close or open the passage to confrontation by holding the dishes together or apart, respectively (Fig. 1, A).

CONFRONTATION STUDIES

Species studied.

At Tall Timbers over 75 species of ants were collected from different habitats (see Appendix I and Fig. 2). The following 28 were selected for the confrontation studies. The habitats of each species are mentioned prior to discussing its defensive behavioral patterns.

Taxon	Symbol used in behavior description
A. Ponerold Complex	
a. Subfamily Ponerinae	
1. Tribe Ponerini	
Hypoponera opaciceps (Mayr)	*H*
Leptogenys manni Wheeler	*Lm*
2. Tribe Odontomachini	
Odontomachus ruginodis Wheeler	*O*
b. Subfamily Dorylinae	
1. Tribe Ecitonini	
Neivamyrmex opacithorax Emery	*N*
c. Subfamily Myrmicinae	
1. Tribe Myrmicini	
Aphaenogaster texana carolinensis Wheeler	*A*
Aphaenogaster tennesseensis (Mayr)	*At*
Aphaenogaster ashmeadi Emery	*Aa*
Pheidole dentata Mayr	*Pd*

	Pheidole morrisi Forel	*Pm*
	Solenopsis geminata (Fabricius)	*Sg*
	Solenopsis invicta Buren	*Siv* Markin et al. (1971)
	Solenopsis pergandei Forel	*Sp*
	Pogonomyrmex badius (Latreille)	*Pb*
2. Tribe:	Attini	
	Cyphomyrmex rimosus manatus Mayr	*Cr*
	Trachymyrmex septentrionalis (McCook)	*Ts*
3. Tribe:	Crematogastrini	
	Crematogaster atkinsoni Wheeler	*C*
	Crematogaster ashmeadi Mayr	*Ca*
	Crematogaster minutissima Mayr	*Cm*
B.	Myrmecioid Complex	
a. Subfamily:	Pseudomyrmecinae	
	Pseudomyrmex pallidus F. Smith	*Pp*
	Pseudomyrmex brunneus F. Smith	*Pb*
b. Subfamily:	Dolichoderinae	
1. Tribe:	Tapinomini	
	Iridomyrmex pruinosus (Roger)	*Ip*
	Conomyrma flavopecta (M.R. Smith)	*Cf*
	Conomyrma insana (Buckley)	*Ci*
c. Subfamily:	Formicinae	
1. Tribe:	Formicini	
	Formica schaufussi dolosa Wheeler	*Fs*
	Lasius neoniger Emery	*Ln*
	Paratrechina [*Nylanderia*] sp.	*P*

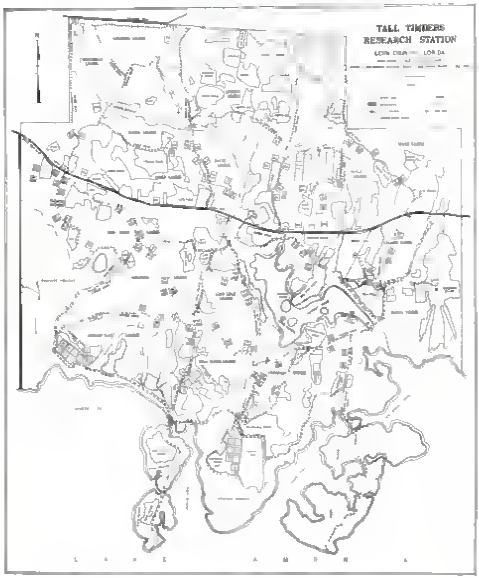
2. Tribe Camponotini

Camponotus abdominalis floridanus (Buckley) Ca*f*

Camponotus (*Colobopsis*) *impressus* (Roger) *Co*

Figure 2. Map of Tall Timbers Research Station Area.

Ants were collected from ecologically diverse habitats such as mesophyllic climax communities (Woodyard hammock, Fraction hammock, Anders Branch), lakeshore vegetation (Hall Island, Sheep Island, Gannet Pond), monotypic pine hammocks, fallow and cultivated fields, weekly and biweekly mowed lawns (Beadle Course, Introduction Field), annual burn areas, fire lanes and roadsides.


TALL TIMBERS
RESEARCH STATION

RESULTS OF CONFRONTATIONS

SUBFAMILY: PONERINAE

Tribe: Ponerini

Hypoponera opaciceps (Mayr)

Habitat:

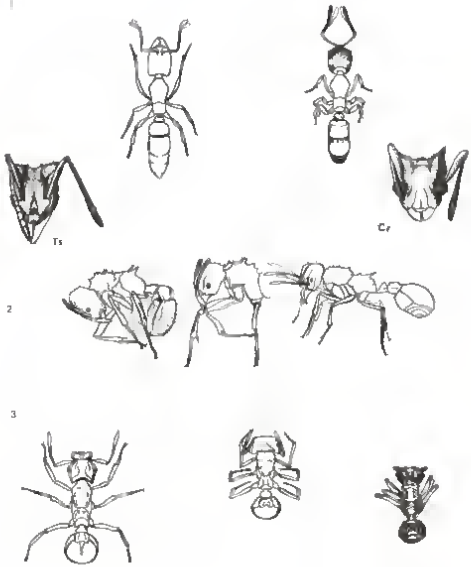
H. opaciceps was especially abundant in hardwood hammock but was not uncommon in cultivated and open fields. This was a terrestrial ant, found nesting in organic peaty soil, under rotting bark, in corn stalks, in accumulated crotch litter of trees, and at tree bases. Colony size ranged from 40-280 individuals. The nests had 10-13 small, 1-2 mm diameter openings at about 3-10 cm apart and arranged in a circle. The queen is indistinct from the monomorphic workers in form and size.

Colony defense:

A small sized colony of the red imported fire ant (210 individuals) was exposed to a normal sized colony of *Hypoponera opaciceps* (Mayr) (200 individuals). The red imported fire ant (*Sa*) workers were the first to invade the colony of *H. opaciceps* (*H*). The intruding *Sa* workers followed the *H* workers on the nest surface apparently because of their colony odor and movement. When an *Sa* worker antennated an *H* worker, the *H* worker stopped, lowered its posture, held its antennae forward, and brought the funicles close together, bent its head towards the substratum, turned its abdomen downward, and stayed motionless for 2.4 to 5 seconds (Fig. 3, 1).

Figure 3. Aggression-suppression-akinesis (ASA) responses elicited by *Hypoponera opaciceps* (1), *Trachymyrmex septentrionalis* (2), and *Cyphomyrmex rimosus minutus* (3). The responses progressed (from left to right in 1 and 3, right to left in 2) with increased contacts between the confronting species.

Frontal view of *T. septentrionalis* (Ts) and *C. rimosus minutus* (Cr) showing well developed antennal scrobes.


1
Ts
Cr
2
3

Response involving prolonged immobility (akinesis) and associated visual and physiochemical aggression reducing cues was invariably elicited by *H* workers and workers of many other species confronting *S. invicta* individuals. It will be referred to as "ASA" (Aggression-Suppression-Akinesis) response henceforth.

The *Lfa* worker opened its mandibles following antennation of the *H* worker, crawled over its dorsum, and attempted biting at its abdomen, petiole, thorax and head. The *Lfa* worker either moved away following initial few bites, or continued biting until the *H* worker moved its antennal funicles. The movement of antennae was followed by raising the body, and swift locomotion. The *Lfa* which had crawled over the *H*, either fell from it and followed the moving *H*, or attempted to continue biting. The swift moving workers of *H* were followed by more than one *Lfa* and were attacked severely. The body parts, such as the head and gaster, were severed from the thorax in all the attacked *H* individuals. However, about 33.2% of the workers (average of 5 colonies) escaped attacks for the first 30 minutes. These workers showed especially effective ASA response.

The *H* individuals are half the size of the *S. invicta* majors. On confronting the majors of *Lfa* they ceased locomotion, but as soon as the majors stopped and antennated them, the *H* workers crawled underneath the majors' bodies, and escaped further bites. *H* individuals then moved faster and entered any one of the nearest nest openings.

While part of the *Lfa* workers attempted a surface assault, others dug out the nest openings of *H. spurcaps*. All the *H* individuals inside the nest congregated deep in a cell and moved their brood and callow workers with them. The pupa-carrying *H* workers followed the others and as soon as one of the workers touched the pupa-transporting worker's

forcibles, it stopped, so did all the following workers. Thus an aggregation was formed in the deeper cells of the nest. After 15-20 minutes, the aggregation broke up and the workers escaped through many neat openings. In response to the escaping *H* individuals, the *Lfa* workers lowered their heads and bodies, made slow antennal movements toward the site of the nearest passing *H* worker, raised their abdomens and continued vibrating them. Similar gaster-moving posture was followed first by the nearest *Lfa* worker, and the response passed on to other nearby *Lfa* workers. About 50% of the *Lfa* workers showed this response within 15 seconds.

Sound production in *S. invicta* was often associated with upward and downward movement of the gaster. The movement of the gaster was not uniform, and continued for 10-35 seconds at odd intervals. The gaster flexing *Lfa* oozed droplets of venom at their stings. The *H* workers exhibited an alerting, random movement, at times even leaving their brood behind. They encountered and were attacked by many *Lfa* workers. The bitten *H* workers curled their abdomens in an attempt to sting the heads of the *Lfa* workers. The stung *Lfa* released their bite but stung the *H* worker before leaving. While the stung *Lfa* showed crippled locomotion for 3-15 seconds, the stung *H* workers showed it for 30-240 seconds. The *Lfa* workers recovered but the *H* workers died within 12-60 minutes. In four assaults, the *Lfa* workers continued stinging the *H* individuals 10-13 times.

During aggressive attempts, 6% of the *H* workers were severed at the head, 32.7% at the petiole, and 18% at the legs. Sometimes the *Lfa* mandibles slid over the cuticle of *H* individuals, and the *H* individuals escaped. Sixty-eight percent of the dead *H* workers were found unsevered. Whenever *Lfa* workers were stung by the *H* individuals, the *Lfa* workers

repeatedly groomed their antennae, dragged their legs as they moved, attempted to bite soil crumbs and any *H* individual encountered. They were more aggressive, biting for the first 3 minutes.

The callows of *H* were stung and carried to the nest by the *Lfa* workers. The brood was similarly used as food. An equal size *S. invicta* colony took over the *H. opaciceps* colony within 3 hours.

Confrontation Index

A simple numerical confrontation index was calculated by exposing 150 *H. opaciceps* workers to 50 *Lfa* workers. In 5 repeated exposures, 706 *H* workers were killed as opposed to 95 of the *Lfa*. The confrontation index was 7 (7.37) for the exposure time of 6 hours. A C.I. for 24 hr confrontation was 7.2, *i.e.*, for every *Lfa* worker killed, 7.2 *H* workers were killed. For stratified data on C.I. of this and subsequent species, see section on "Confrontation Index" and Appendix 7.

Leptogenys minna Wheeler

Habitat:

Nests were found in rotted logs with high moisture content, in duff on the ground, and crotches of oaks. The ants aggregated in clusters of 1100 to 2300 workers. Queens had slightly larger abdomens and rounded petioles than workers. No other sexual dimorphism was apparent. They were normally found in mesophyllic hammocks, lakeshore woodlands and creek woodlands.

Colony defense

Colonies of *Leptogenys minna* consisting of over 2000 individuals were exposed to *S. invicta* colonies of the same size. Minor *Lfa* workers

were the first to encounter the foraging *L. minutum* (*L*) individuals. The *Solenopsis* touched its antennae to those of *L* and retreated. The *Solenopsis* turned to a sister worker and touched her scape and then apical flagella with its antennae. The *Solenopsis* encountered raised its head and held its antennae parallel. After about one second it turned to another sister worker and repeated the antennation. The same ant antennated many *Solenopsis* workers and the "message" was transmitted. A small part of the *Solenopsis* colony was agitated as soon as the messenger ants reached the colony. Within 3 minutes, 20 minors and 3 majors invaded the *L* colony. This pattern of "aggressive message transmission" was common with the fire ant and was seen prior to its invasion of any alien ant colony.

As soon as the *Solenopsis* worker approached, the *L* workers curled their abdomens and stridulated. The stridulatory file of *L. minutum* consisted of about 50 extremely fine, parallel ridges at the base of the second tergite which forms a constriction. The edge of the first gastric segment scraped on the file and produced sound (Fig. 4). The sound was an audible "hiss." The stridulatory response was first transmitted to the nearest workers and then to the whole colony. At first antennal contacts were not involved either between the sister *L* workers or between the *Solenopsis* and *L* workers. The *Solenopsis* workers opened their mandibles, and grabbed the stationary, stridulating *L* workers at their thorax, abdomen and petiole. The *Solenopsis* workers continued biting at several places at the *L. minutum* cuticle. The *Solenopsis* workers biting at the abdominal region of the *L* were brushed off by the *L* workers with their hind tibiae and tarsi. *L* has a long sting and it curled its abdomen to sting the fire ant ventrally as well as laterally but never dorsally. The stung *Solenopsis* let go of the abdomen but still held the *L* appendages. It eventually stung the *L*.

The stung *L* workers showed slow antennal movement and leg paralysis. However, they stridulated and continued to antennate the sister workers. The "hissing sound" was again transmitted throughout the colony, and the colony was agitated. Within 10 seconds, the *L* workers lifted their larvae and pupae between their mandibles and placed them between their legs and transported them.

The *A. fa* workers followed the escaping *L* workers and attacked and stung them. The antennae were not attacked since they were held upwards. The callows were the first to die after stinging. The heads of such workers were removed and the rest was carried to the nest. Many majors (over 6%) were trailed with the *A. fa* minors, and they mostly transported crippled, live *L* workers, their centipede food, and larvae. The pupal cocoons were opened and transported to the nest.

L workers are 1-1.3 cm long and 0.2 cm wide. Their sting can reach the mouthparts ventrally, and up to the postpetiole laterally. Despite the fact that when killing a centipede (2-3 cm long) the *L* sting could be protruded 1-1.5 mm, it was never seen to pierce the *A. fa* cuticle. There was no topical poisoning due to the *L* sting.

S. invicta minors were more aggressive to *L* workers. They opened their mandibles as the *L. minimus* workers passed by and touched any of their body parts. The hind legs of *L* were grasped by the *A. fa* minors that held onto them even after repeated attempts to dislodge by the *L* workers. The attacked *L* communicated with encountering *L* by antennal contacts after which the latter moved away even faster. Small aggregates of 10-15 *L* workers were seen to form after 20 minutes. These were also effectively attacked by the *A. fa* minor.

The stung *L* workers shook their bodies, stretched their trochanters,

and dragged their legs. When stung more than 4 times they slowed their antennal movement, fell on the side, and opened and closed their mandibles several times. The *L* workers curled their abdomens when the *Lfa* poison was topically applied. In 15% of the cases the antennae of *L* were severed at their pedicels.

Confrontation index

A simple numerical index was calculated by exposing different proportions of *Lfa* and *L* workers in petri dishes. It was found that 1860 *L* workers were killed by 80 *Lfa* workers in 6 hours. The confrontation index was approximately 1:23 (1:23.25). However, it approached 1:1 after 24 hr confrontation.

Tribe: Odontomachini

Odontomachus rugosodis Wheeler

Habitat:

O. rugosodis was most abundant in moist mesophyllic hammocks. It was also found in pecan groves and at the base of many trees in open areas. This terrestrial species tends to require high moisture micro-habitats. The ant nests in and under rotten wood, leaf litter, pine needles and in peat soil. *O. rugosodis* nests are simple with 1 cm openings, widening to 4-15 cm towards the bottom. Quite often, two nest openings were observed. A mound was found to be built on the opposite side of the tunnel inclination.

Colony defense

When connected to the imported fire ant colony, the ground surface area of the *O. rugosodis* (*O*) mound was first explored by 3 *Lfa* miners. At first *Lfa* moved at random and gradually gathered by the *O* nest entrance.

Any *O* ant either entering or leaving the nest confronted the *Lo* workers. The first *O* to encounter a fire ant worker stopped, leaned back, antennated the *Ma* vertex, antennae, and petiole for 2-5 seconds, and again leaned back at the same position. It opened its scissor-like jaws, and turned to nearby foraging *O* workers. It communicated (which can be referred to as aggressive communication) by giving 2-3 strokes at the nest-mate's funicular segments and slightly brushing its foretible. The ant receiving the message (on the left in the figure) held its antennae between the antennae of the messenger ant (on the right in the figure) and opened its mandibles when the antennation was completed (Fig. 4; 2). Antennation during a food find differed from the above since it involved a prolonged (5-10 sec) flagellar contact by the recipient (Fig. 4, 1) and was not often followed by mandibular opening. All the encountered nest-mates were stimulated to disperse to 1 cm around the *Lo*. More *O* nest-mates emerged from the nests and dispersed away from the nest entrance. One of the *O* ants vibrated its body and this motion was followed by 90% of the nest-mates, and to which newly emerging *O* workers responded by opening their mandibles. Body flexing was considered as "distress signal" since *O* individuals surrounded the *Lo* workers but did not attack them. As the number of *Ma* workers entering the *O* nest increased, this signal increased in frequency. If the *Lo* workers were deliberately removed, body flexing in *O* ceased. After 6 minutes the *O* workers moved to the *Lo* individuals, antennated them, leaned back, again antennated, leaned forward and immediately snapped shut their mandibles on the spot they antennated. Such spots involved the head, thorax or petiole of the confronting *Ma*.

During antennation by *O* the *Ma* ceased locomotion, held its antennae upwards, moved them slowly up and down alternately, flexed its abdomen

Figure 4. Confrontation behavior between *Odontomachus ruginodis* and *Solenopsis invicta* workers.

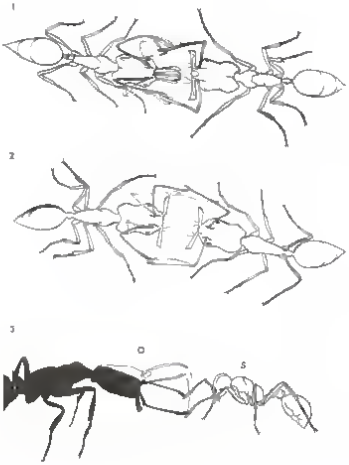
1. Antennation between a messenger *O. ruginodis* worker (right) and a recipient worker (left) during a food find. The inner and outer portions of the messenger's flagella were contacted by the recipient worker for a prolonged period and it opened its mandibles only slightly

2. Aggressive message transfer involved momentary contacts of the apical flagellar portions between the messenger and the recipient and was followed by the recipient's opening of its mandibles.

3. Recognition antennation between *O. ruginodis* (O) and *S. invicta* (S) involved contacts of the flagellar clubs of *S. invicta* to the apical flagellar portion of *O. ruginodis*. *O. ruginodis* raised its antennae, opened its mandibles, and retreated.

4 Following a second antennation between *S. invicta* and *O. ruginodis*, *S. invicta* attained a gaster-flexing posture. *O. ruginodis* antennated the flexing gaster and snapped its mandibles at the petiole, severing it from the alitrunk.

5. *S. invicta* worker crawling onto the *O. ruginodis* worker, seizing its mandibles and stinging it.


1
2
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O

rotating it through 5 mm sideways and 1.5-2 mm upwards and downwards. More than one *O* moved towards the *Ifa*, flexing its abdomen, indicating a visual or visuo-chemical stimulus.

The mechanism of mandibular closing in *O. rugineda* was investigated. There are 8 long (1-1.5 mm being the longest) sensory setae along the mandibular incisory edges of *O* workers (Fig. 5, top). When the mandibles are open to 180° these hairs project in front. The frequency of mandibular closures was more towards the alien species such as *Ifa* workers than towards dental stick. It can be seen from Table 1 that removal of both of the antennae of an *O* worker lowered mandibular closures contrary to the ant with both the antennae intact, with or without mandibular hairs. Also, when apical flagellar segments were coated with paraffin wax, the mandibular closure reduced in number. Antennation occurred prior to such action. Also, there was a pause of 0.3-0.5 seconds between antennation and the closing of the mandibles.

O. rugineda workers rotated their heads through 30° to either side while their mandibles were open to 180°. The ant's mandibles covered the entire front portion of its thorax facilitating attack and defense by turning the head without actual locomotion. In spite of this well adapted defense mechanism, *O* workers cut their own fore- and mid-tibiae. Workers used their mandibular closing mechanism for escape. They are capable of springing themselves as far as 28 cm and as high as 8 cm by closing their mandibles on a hard substrate. Even ants attacked at their appendages by the *Ifa* workers were able to somersault. Escape response was much more apparent as confrontations with alien species increased. *Ifa* workers attacked even the mandibles and held on to them. No snapping of mandibles was seen in such cases (Fig. 4, 5). It was also

seen that as the *O* closed its mandibles on the *Lfa* workers, the *Lfa* workers were tossed up to 35 cm away from the *O* worker. No attempt was made to sting, although *O. rugithorax* possesses a well developed sting.

S. invicta attacked the antennae, mandibles and legs, all of which are long and easily accessible. However, the *Lfa* workers were unsuccessful in attacking the smooth, spine-like petiole of *O*. The *Lfa* workers first flexed their abdomens and poison droplets oozed at their stings. Within 3 minutes they ceased gaster-flexing and attempted biting the *O* workers. This response was apparently due to the frequent mandibular attacks by *O*. The *O* workers that were directly stung or were smeared with venom, dragged their legs and died within 1.5-2 hours. Biting by *Lfa* ensured the quick penetration of venom into the *O* cuticle. The *O* workers that were attacked at their flagellar joints made a random movement and did not snap their mandibles showing the possible effect of secretions from the sting and mandibles on the antennal innervations, and eventually on the mandibular closure, similar to the results in Table 1. The venomed *O* worker groomed its antennae and body parts. This also increased apparent smearing of venom to the mouth parts and elsewhere.

In spite of heavy initial kill of the *Lfa* workers within 3 hours (344 *Lfa* - 27 *O*) because of its large worker force, the *Lfa* overcame the *O* colony. The alate, hermless males and queen were carried away as food. The *Lfa* workers severed the gasters of the dead *O* workers, but did not carry them into their nest. The pupae were removed from cocoons and both pupae and brood were used as food. If less than 100 *Lfa* were exposed to about 500 *O* workers, the *Lfa* workers were killed and piled up as refuse by the *O* workers.

Table 1 Mean number of mandibular closures shown by *Odontomachus ruginodis* to imported fire ant workers and dental stick (n = 10)

Parts removed from *O. ruginodis*	*S. invicta*	Dental stick
Left flagellum	4.1	3.0
Right flagellum	5.9	2.6
Right and left flagella	0.2	0.1
Apical flagella coated with wax	3.8	1.5
Mandibular hairs removed	5.8	2.5
Ant with mandibular hairs and antennae	7.5	2.8

For analysis of above data and treatment differences, see Appendices 2 and 3

Escape response

Odontomachus showed a greater number of backward somersaults in response to increased numbers of confrontations with *Lfa* workers. If the proportion of *Lfa* was twice that of *O*, there was immediate escape response. First the *O* individuals showed mandibular ticking by clapping them against each other. They moved fast, raised their antennae and made circular movements. Apparently, the ants stridulated feebly by rubbing dorsal cuticle of the first gastric segment on the grooves of the second gastric segment which otherwise forms a feeble constriction between these segments in this ponerine (Fig. 5, bottom). The stridulation and ticking followed general movement of *O* individuals away from the nest entrance.

Some ASA response was shown by the escaping *O* workers when they encountered the *Lfa* workers. They immediately stopped, closed their mandibles, held their antennae near the head and made no movement for 10-30 seconds. The *Lfa* worker antennated such *O* individuals and moved away. However, as soon as *O* made some movements, the *Lfa* workers attacked them at their appendages. The escaping *O* workers made no attempts to defend themselves and ran at random. The *Lfa* workers attached themselves to the *O* appendages, stung them and finally killed them.

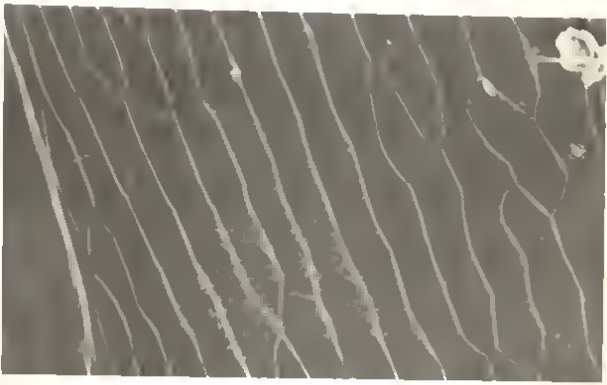
Confrontation Index

In *O. rugiventris* confrontation index studies revealed data contrary to the earlier species. In a replicated experiment, a total of 1500 *O. rugiventris* workers confronted 3000 *S. invicta* workers. After 24 hours, mortality of *O. rugiventris* was 442 against 2495 of the *S. invicta* workers. C.I. was therefore 0.177, i.e., about 5 *S. invicta* workers were killed for each *O. rugiventris* worker.

Figure 5. Profile of *Odontomachus rugosodis* with open mandibles. Sensory hairs (T) can be seen on the mandibles (MD). (Magnification 50X) (Top).

Cuticular asperities at the base of the 2nd gastric tergite of *O. rugosodis*. (Magnification 1120X) (Bottom).

ODONTOMACHUS AUCTORIS WHEELER



SUBFAMILY: DORYLINAE

Tribe: Ecitonini

Neivamyrmex opacithorax (Emery)

Habitat:

General habitat is humid mesophyllic hammocks. They are terrestrial ants, found raiding other ants in open cultivated fields. Raiding and emigrating columns were found in the lakeshore woods, and bivouacs were collected from rotted wood in the Fraction hammock and Ander's Branch. This species is polymorphic, and colonies often consist of over 10,000 workers and one queen. In the laboratory the colonies formed raiding columns at about 5:30 a.m. and 6:00 p.m. In December 1971, they piled prey catches consisting of dead insects within the Wilson cell. Callows were not seen to join the foray. Except for the raiding and foraging times, the ants clustered in the Wilson cell and licked the queen. Callows were found to stay around the larvae and the old workers would carry the brood if the colonies were disturbed.

Colony defense

One colony of *N. opacithorax* (*N*) consisting of about 10,000 workers and a physogastric queen was connected at 5:40 p.m. to a *Solenopsis invicta* colony of almost equal size. Passage between the colonies was opened at 5:55 p.m. on July 6, 1971, and confrontation behavior was seen.

Fire ants and the *N* workers confronted near the *Sin* colony. The confronted *Sin* rushed back, stroked the antennae of the encountered forager, and within 5 minutes the whole *Sin* colony was agitated. Apparently, there was tactile stimuli that caused the alarm behavior. The *Sin* nest entrance was full of workers rushing out. They blocked the intruding *N*

workers which dispersed their column. Increased rate of locomotion was observed in the *N* workers that broke their single-file formation.

The *Lf* that encountered major or minor *N* workers ceased locomotion, suddenly raised their gasters following the opening of their mandibles (threatening behavior), and waved their antennae slowly towards the moving *N* workers. Over 50% of the encountered *Lf* raised their gasters vertically, secreting venom at the tip of their sting. Within 4-5 minutes the *N* workers attempted to bite the gaster-flexing *Lf* workers with their mandibles. However, 66% of the time the attacking *N* retreated and randomly moved away from the *Lf* workers. The disturbed *Lf* workers stopped flexing their gasters and pursued the *N* workers. Any *N* worker encountered was bitten repeatedly at the cervix, petiole and gaster. The *Lf* minors crawled over the *N* workers (1.1-1.4 mm long) and repeatedly bit them on the gaster, petiole, thorax and cervix. The bitten *N* stopped and attempted to extricate itself from the *Lf* mandibles. The *N* slowly gripped the legs, moved forward, turned its head down and raised its antennae upwards, apparently extricating itself forcefully. The *Lf* worker was not seen to sting for 0.3-0.7 seconds. This time interval was sufficient for 27.3% of the attacked *N* to escape. No akinetic response was shown by the *N* workers. In 3% of the cases, the *Lf* workers attacked the mandibles of *N* within the first 20 minutes of attack response. In almost all cases, the mandibular grip was released within 30 seconds and the *N* escaped. During these encounters, the *Lf* majors, minors, or media were invariably stung by the *N* workers. The stinging *N* opened their mandibles, stood up on their legs, and curled their gaster forward under their body. However, the *N* workers were not aggressive towards *Lf* and only defended themselves. Fire ant workers after being stung were found to recover and be on their

legs again within 5 minutes. However, if they were repeatedly stung (5 times or more), they would bite on soil particles. This response was followed by slow and crippled ambulatory movement, and they died within 30 minutes.

The *N* workers were first bitten 7-10 times before they were cut and torn apart into pieces. Repeated biting by *L. fa.* was accompanied by stinging. *N* workers, after being stung, moved faster, waved their antennae swiftly, and within 3 minutes repeatedly hit their head on the ground. These twitching ants attracted more *L. fa.* workers. Two *L. fa.* workers attacked and removed the legs of these ants. Any workers stung more frequently showed no movement after 10 minutes and died. Repeated attacks by *L. fa.* killed a large number of *N* workers that would have otherwise escaped.

The callows and physogestric queen remained passive. Workers guarding the queen were reduced in number from 30 to 5 within 3 hours as the assaults by *L. fa.* progressed and more and more *L. fa.* workers invaded the *N* colony. As soon as the callows were attacked, the agitated *N* workers carried their pupae, callows, eggs, larvae and catches in their mandibles. The ants moved clockwise inside the Wilsen cell for 2.5 hours. The queen moved slowly and was guarded by about 10 *N* workers around her.

The invading majors and minors of *L. fa.* stayed around the milling *N* workers keeping their mandibles open and bit the encountered *N* workers. Finally, the *L. fa.* workers made their way to the physogastric queen, attacked the guards and crawled over the queen. The queen left her mandibles open while milling but made no attempts to bite the attacking *L. fa.* She was stung at her enlarged gaster repeatedly for 15 minutes before she became immobile. The gaster was severed from the rest of the body and was torn open. Pieces of gaster and the dead *N* workers were transported

by the *L.f.a.* majors and media workers to the *L.f.a.* colony. All the milling *N* workers were attacked one by one and were killed. Two hundred fire ants were killed as opposed to the whole *N* colony within 18 hours of confrontation.

Escape response

Milling was considered a response prior to escape (under laboratory conditions), it was associated with the peripheral *N* workers running outwards. It was seen that such escaping workers laid trails and were followed by 10 *N* workers. Only one out of five *N* colonies showed milling. In other cases, *N* workers moved the brood, catches, and the queen (shifting of bivouac) away from the invading *L.f.a.* workers. The transporting *N* workers were attacked by the *L.f.a.* and the brood and callows were carried to their own nest. When the columns of escaping ants were broken due to *L.f.a.* attacks, the *N* workers moved into small files of 2-10 workers and were easily victimized.

Confrontation index

In five repeated experiments, 383 *L.f.a.* workers subdued 2363 *N* workers within 24 hours. The confrontation index was 6.17.

SUBFAMILY MYRMICINAE

Tribe: Myrmicini

Aphaenogaster texana carolinensis Wheeler

Habitat

A. texana carolinensis was found to inhabit climax mesic hammocks in North Florida. This species excavates simple 2-35 cm deep tunnels and builds a mound on one side of the entrance hole. On rainy days, the brood and queens were seen to be moved to adjacent semirotten logs. This appears to be a high moisture adaptation. *A. texana carolinensis* was found in association with termites as well as such ant species as *Prenolepis dentata* Mayr and *A. tennesseensis*, but never nesting together with these other species. When disturbed, it devoured termites, otherwise it foraged on a variety of arthropods. *A. texana carolinensis* was not seen dwelling in arboreal habitats. Colonies average 126 to 750 individuals.

Colony defense.

Many colonies of *A. texana carolinensis* (A) were exposed to *S. invicta* (*Sa*) and the following confrontation pattern was typical.

On September 9, 1971, a colony of 700 A workers was exposed to a normal sized colony (1500 individuals) of *Sa*. *Sa* workers laid a recruitment trail to the A colony within the first 30-35 minutes. One media and one minor worker were seen at the nest opening of A after 47 minutes. The *Sa* workers apparently oriented to the nest opening from a distance of 4 cm. As soon as the minor touched its antennae to those of the A worker at the nest entrance, the A retreated inside, stroked the flagellar portions

of its antennae to a nest-mate and again came up to the nest entrance. The flagellar streking response was transmitted throughout the colony within 10 minutes. The queen and the general workers were seen to move the brood into the lower cells. About 32 normal A workers accumulated in the entrance tunnel, they opened their mandibles as they approached the entrance. The *Af* workers pushed their heads into the 0.7 cm A nest opening, kept their mandibles open, moved away from the opening making random circular movements. These movements were slow but were accompanied by aggressive communication involving antennal contacts with any encountered *Af*. Within 2 hours, 3 majors, 5 minors and media of *Af* were seen at the A nest entrance. Two A workers emerged from the nest opening after 2 hours. The *Af* at the nest entrance attempted to grasp the A antennal flagella which were immediately raised straight upwards as a protection. The A worker grasped the mandibles of the *Af*, curling its abdomen beneath its thorax at the same time, raising its legs, and reaching its sting to the *Af* ventrum. The whole action was sometimes completed within 0.3 seconds and lasted for not more than 10 seconds. The *Af* released its mandibular grasp and curled its body. A temporary, 15-20 minute paralysis was observed in the attacked *Af* workers. The 2 A workers approached all the *Af* workers at the nest entrance and repeated the same behavior and paralyzed them. The paralyzed workers were not attacked until they recovered. Three majors were seen to recover within 5 minutes and were stung again. They immediately showed paralysis and never recovered. The minors recovered slowly. Two of them returned to their colony and caused agitation in the colony. After 2.33 hours, series of *Af* majors, media, and minors trailed to the A colony. The *Af* workers confronted the A workers outside the nest and showed intensive

attack responses. They opened their mandibles and immediately bit the A appendages. The A workers raised their antennae parallel to each other and exhibited an ASA response. They brought their legs together, lowered their heads and abdomens, then slowly brought their antennal flagella close to the scapes on the antennal sockets. The *L.fo* workers continuously bit the A workers but did not sting.

The ASA response lasted for 4-32 seconds. It was followed by the escape response. The A near the nest entrance entered it and touched the flagella of any A workers encountered in the nest; the whole colony was agitated. During the next 25 minutes, the queen, teneral s, and the brood were moved to the upper tunnels of the A nest. The A workers in the entrance tunnel emerged one by one and exhibited stinging posture as soon as they encountered the *L.fo* workers. They were followed by a number of *L.fo* workers and attacked at their appendages. Topical application of A venom paralyzed many attacking *L.fo*. Only 3 *L.fo* were seen alive in the 3 cm diameter vicinity of the A nest entrance. One A individual reentered the nest and reached the brood cell. There was some colony agitation and about 50% of the colony swarmed out of its nest after 2 hours and 5 minutes. The swarming A workers included 35.3% tenerals, and carried larvae and pupae in their mandibles. Queen and alates were not seen to swarm.

The swarming individuals showed ASA response and moved faster as soon as the *L.fo* moved away. However, no attack responses were shown by tenerals and very few by the adults. The swarming ants were bitten on their legs and stung at this point by the *L.fo* workers. The *L.fo* venom affected the A workers comparatively slowly. The A workers that had been stung did not sting *L.fo* workers, but groomed their own antennae

continuously, and were also seen to lick the cuticle where the *Lfa* sting had penetrated. Within 3.5 minutes the *A* workers curled their hind legs beneath the body and fell on the side. They had not recovered after 13 minutes. All the swarming workers were attacked. However, some workers reentered the nest and stayed at the entrance as guards. No activity was noticed in the *A* nest for the next 6 hours and 27 minutes, when again the colony was agitated and a second swarming was observed. It involved 63 tenerals and 110 workers carrying brood. Only 25% of the colony stayed inside, including the queen and a majority of tenerals. The alates joined the swarm. Each swarming alate was followed by more than 1 *Lfa* and flicked its wings as the *Lfa* crawled on the *A* dorsum. Prior to the wing flicking the alates escaped *Lfa* stings because their tergal region was not exposed. Once it was open to *Lfa* stings they were killed easily. When all the swarm was killed, the alate queens and the *A* brood were transported by the *Lfa* workers to their nest. No invasion of the *A* nest was observed.

A third swarm was seen after one hour. Queen and brood carrying tenerals emerged from the nest and were attacked by the *Lfa* workers. There were no attack responses shown by the queen and the *A* workers.

Confrontation Index:

One thousand *A* workers were exposed to a similar number of *Lfa* workers. A 24 hour confrontation showed an index of 0.436, i.e., 2 *Lfa* workers were killed for each *A* worker.

Aphaenogaster tennesseensis (Mayr)

Habitat

A. tennesseensis inhabited comparatively humid, open areas of meso-

phyllic hammocks along the lakeshores. It nested at the base of oak tree trunks in 16-50 cm deep cavity-like nests, or extended their terrestrial nests to adjacent rotted logs. The nests were also found in 7-10 cm wide cavities under the bark of dead oaks, about 1-3 meters from the ground. The colony size varied from 123-700 individuals, had one fertile queen, and in August and September several alates were seen.

A. tennesseensis workers individually foraged on live oak trunks. On the same tree, *S. invicta* trailed cryptically along the trumpet vine (*Campsis radicans* (L)) stems or through the bark crevices. Occasional confrontations between these species were observed on September 31, 1971. *A. tennesseensis* forays carried spiders, termites, hemipterous, orthopterous, coleopterous, lepidopterous, and dipterous insects.

Colony defense:

When the passage between a *S. invicta* (*Si*) colony and *A. tennesseensis* (*At*) (700 workers) colony was opened at 11:00 a.m. September 31, 1971, *Si* workers laid a recruitment trail. Minors were the first to forage. Several back and forth forays continued until 11:15 and one minor *Si* reached the *At* colony at 11:50. It retreated and transmitted the message to workers behind it and to the *Si* colony. The first confrontation between the *Si* and a foraging *At* worker was observed at 12:05. The *Si* worker antennated the *At* worker, opened its mandibles, bit the long antennae of the *At*, and slightly curled its gaster between its legs attempting to sting. Before the *Si* worker could sting, the *At* worker bent its abdomen beneath its thorax, raised its legs, and projected its sting until it reached the cuticle of the *Si*. Apparently, the venom was applied topically. The *Si* worker released its mandibular grasp, curled its gaster, held its legs together and stayed in a paralyzed condition for

21 minutes. At 12:10, thirteen *L. fla* minors and media were seen to reach the *At* nest surface. The *At* worker antennated the other nest-mates near it and slowly moved towards the *L. fla* workers. It antennated any *L. fla* workers encountered, raised its legs, curled its abdomen either sideways or beneath the legs reaching one *L. fla*, then stung the *L. fla* and turned to another *L. fla*. Every *L. fla* worker when stung showed paralysis and dropped dead. The stinging response in *At* was associated with its antennation of the *L. fla* antennae (63% cases) or any other body part. In 72% of the cases, the sting was directed towards the *L. fla* worker by curling its gaster. However, in 28% of the cases, the *At* workers grasped the aggressive *L. fla* at its cervix, head or thorax with its mandibles and then stung. Projection of the sting was so brief that piercing of the cuticle was not apparent.

The *L. fla* workers exhibited no sting or gaster-flexing posture during initial 30 min - 2 hr of confrontation. The lack of response may be attributed to an *At* secretion that inhibits such responses. However, they opened their mandibles, attempted biting the *At* worker's antennae, and before the *L. fla* could hold its antennae, the *At* worker stung and paralyzed the *L. fla* worker. A single *At* worker was seen to paralyze 12 3 *L. fla* media, minors or majors (mean of 20) within 20 minutes. With a slight touch of *At* venom, the *L. fla* worker was seen to retreat, bend its head, touch its antennae to the ground, and walk backwards rubbing the antennae. It showed leg paralysis and fell on its side. The paralyzed *L. fla* showed slight leg movement after 45 minutes, but was not stung by the *At* workers until the *L. fla* recovered to walking posture. The *L. fla* that was stung twice died immediately after the second sting; however, those stung only once recovered. The stinging and recovering continued for 2 hours on the *At*

nest surface. At 1:15 a large trail of *Lfa* was seen on the above ground part of the *Af* nest. The outnumbered *Af* workers showed escape response to the *Lfa* invaders. After 30 minutes, *Af* workers showed an ASA response, similar to *Hypoponera opaciceps*. Whenever approached by the *Lfa* worker, the *Af* worker turned its head down, placed its antennae on the ground, brought its legs close, bent its gaster down and stayed motionless for 12-125 seconds. The *Lfa* crawled over it and bit its thoracic, abdominal, or petiolar portion. However, if the *Lfa* bit the antennae, the *Af* worker immediately moved away. The moving *Af* did not show stinging response and was grasped at its appendages, then stung by the *Lfa* workers around it. About 69 *Af* workers were killed on the nest surface. Three entered their nest and the colony was agitated. A part of the colony including alate queens and males swarmed out of the nests. The *Af* workers showed stinging responses and killed many *Lfa* workers. During 4.5 hours (4:20 p.m.), 511 *Af* workers were killed by *Lfa*. The *Af* workers on the nest surface showed a continuous gaster-flexing for 2-3 minutes except a group of surrounding *Lfa* workers. The gaster-flexing gradually slowed and finally stopped, at which time 16 *Af* workers were stung by the *Lfa* workers.

The rest of the *Af* nest-mates swarmed at 10:00 p.m. The queen, brood carrying *Af* workers, and teneral were killed by the *Lfa*. The queen showed no apparent attack response, but showed an ASA response similar to workers. Antennae and legs of dead ants were removed by the *Lfa* majors and medias. The carcasses were used as food. No flight was observed as an escape response.

In 2 out of 10 nests studied, the *Af* workers reentered their nests and reswarmed after 15 hours, the struggle continued for as long as two days. Swarming was considered as a mass-escape response, and the ASA

response a defense mechanism prior to escape. *Lfa* venom was fatal to the *Aa* workers. They were seen to curl their legs and die within 13-20 minutes. Although the *Aa* venom was toxic to the *Lfa* workers, paralyzing and killing many of them, the *Aa* colony was subdued because of the continuous invasion by the outnumbering *Lfa* workers.

Confrontation Index

The *Lfa* kill was in a proportion of 785 to 261 of *A. tennesseensis*. The index of aggression was less than 1, i.e., 0.337. In other words, more than two *Lfa* were killed by each *Aa* worker.

Aphaenogaster ashmeadi Emery

Habitat

A. ashmeadi (*Aa*) inhabits comparatively xeric habitats and is common to turkey oak associations. This species was collected from Hall and Sheep Islands at Tall Timbers. The ants were seen foraging individually for insects, termites and spiders. In a few cases a 0.5 cm mound was seen around the 0.3 cm nest entrance. The ants were more active nocturnally and on overcast days. About 200-500 workers were collected from a single mound. Usually a single queen was present.

Colony defense

A colony raised in a vertical ant nest was exposed to a normal (1500 individuals) size *S. invicta* (*Lfa*) colony in the laboratory on September 16, 1971. During the first half hour the *Lfa* minors laid a recruitment trail and about 7 minors and media entered the above-ground nesting area of *Aa* after 40 minutes. The first response shown by the *Aa* workers was similar to that shown by *A. tennesseensis* workers. The *Aa* worker touched

its antennae to those of the *Lfa* minor, raised its head and thorax, curled its abdomen beneath its thorax until it reached the ventrum of an approaching *Lfa* worker, and either stung the *Lfa* worker or applied its venom topically. The *Lfa* showed initial mandibular opening and biting of the Aa antennae but no stinging. The apparent effect of the venom caused the *Lfa* to release its mandibular grasp and the *Lfa* was seen to curl and remain paralyzed for 10-20 minutes. Aa workers did not attack the paralyzed *Lfa* workers until they recovered. The recovered workers moved and were approached by Aa workers and stung again. The *Lfa* stung twice failed to recover. Within the first hour, 20-25 workers of *Lfa* were killed by 5-7 Aa workers near the entrance. The *Lfa* attacked only at the appendages and stung the Aa workers (3 cases within first hour). All the stung Aa workers curled their hands downwards and fell dead within 13 minutes. The *Lfa* venom was more toxic and fatal, however, the Aa venom paralyzed more *Lfa* invaders. The *Lfa* workers that returned to their nests were not seen to invade the Aa nest for the next 30 minutes and then a large trail was followed. The Aa workers stayed in their nest tunnels. The Aa tenerals showed movement of the brood to the lower nest chamber. The queen was surrounded by about 6 tenerals and proceeded to the lowermost part of the nest. The mature workers congregated in the entrance tunnel, the uppermost Aa held their mandibles open. As soon as the *Lfa* trail reached a 1 cm distance from the Aa nest entrance, the guarding Aa workers attacked their hands, cervices, and thoraces and stung them. The *Lfa* workers showed paralysis, but the *Lfa* workers outnumbered the Aa and attacked the Aa workers' appendages, pulled on them, and stung them. The Aa workers fell dead and were replaced by the Aa in the entrance tunnel. The confrontation continued for 6 hours, 65-87

Lfa workers and about 24-35 *Aa* workers were killed. The *Aa* workers showed no stinging response to the remaining *Lfa* workers. The *Aa* stayed in the entrance tunnel and a swarming response was seen after 6.5 hours. About 33% of the *Aa* workers crawled out of their nest and stayed on the plastic walls. A third invasion of *Lfa* was seen after 6.75 hours. The invading *Lfa* faced less resistance from the guard workers. The *Lfa* attacked the mandibles of the guarding *Aa* workers and pulled them out of the entrance. The *Aa* workers were aggressively stung and killed by the *Lfa* around them. After 30 minutes, the *Lfa* widened the nest entrance. The *Lfa* majra showed gaster-flexing for 2-3 minutes and then crawled to the brood chamber. The *Aa* tenerals were immediately stung and they died within 3-10 minutes. The larvae and the queen were also stung by the *Lfa* workers. The *Aa* queen opened her mandibles, bit the aggressive *Lfa* miners and majra, but the queen was stung on her head. The queen showed no movement after 13 minutes and was dragged by the *Lfa* workers to their nest. The whole colony was subdued by the invading *Lfa* workers within 8-10 hours. However, brood transport continued up to 24 hours.

An ASA response, similar to that of other *Aphaenogaster* species, was exhibited by the escaping *Aa* workers. They brought their legs closer to the thorax, held their antennae in repose, bent their head and abdomen down, and stayed motionless for 30-102 seconds. The motionless ants escaped the *Lfa* stings but were continuously bitten dorsally. Those attacked at their antennae showed some locomotion and were stung by the *Lfa* that crawled on them. The attacked *Aa* did not show stinging response.

Confrontation Index

In 24 hr confrontation experiments, 920 *Aa* killed a total of 1922

Lfa majors, miners and media. The confrontation index was approximately 0.48, *i.e.*, for every 2 *Lfa* killed one *Aa* worker was killed. However, because of the large size of *S. invicta* colonies (practically double *Aa* colonies) they can be expected to subdue any *A. ashmeadi* colony in nature.

Pheidole dentata Mayr

Habitats

P. dentata is especially abundant in mesophyllic and pine barren ecosystems. However, it was occasionally found in open fields. This species usually nested in soil and constructed a 2-25 cm triangular mound with most of the dirt deposited on the outer side of the mound. The species was also found nesting in hardwood stumps and in standing dead timber. *P. dentata* is a oligomorphic species (apparently dimorphic, though a slightly smaller form similar to the large major form was present) with 1300 workers in a normal sized colony and more than one queen. It was found in rotted wood with termites and *Aphaenogaster rudis*.

Colony defense

Colonies of *P. dentata* (*Pd*) consisting of about 800 individuals were exposed to *Lfa* colonies of similar size. The following pattern of aggression and invasive behavior was observed.

The *Lfa* miners were the first to lay a recruitment trail to the *Pd* nesting area. The *Lfa* colony was agitated during the first 20 minutes and a group of 5 miners entered the *Pd* nesting area. Foraging *Pd* miners stopped, waved their antennae and moved about at random. After 2-3 minutes of random movement, they made an undulating but directed movement toward the alien workers. As soon as the *Pd* miners approached within 3-5 cm of the *Lfa* workers, the *Pd* opened their mandibles and retreated. Two of the

5 *Pd* minors reentered the nest and touched either the abdominal dorsum or tibiae of any nest-mate encountered (aggressive communication) with their antennae and mandibles open. Such nest-mates immediately left with their mandibles wide open (alarm response). The *Pd* colony was agitated.

During the next 15 minutes, the proportion of *Pd* majors coming out of the nest increased (31 majors to 7 minors). Meanwhile, another group of the *Lfa* entered the *Pd* nest area. The *Pd* majors held their mandibles open, surrounded the *Lfa* media and minors, swiftly moved forward and grasped the *Lfa* hind legs, severing them at the tibiae. The *Lfa* exhibited a gaster-flexing posture, oozed venom at their stings and remained motionless. The *Pd* majors continued attacking and severing the *Lfa* appendages. The action was swift (less than 0.5 sec) each time they cut the *Lfa* appendages. The gaster-flexing by the *Lfa* attracted the *Pd* majors. The *Pd* majors directed their attacks toward the gaster of the *Lfa*. Eventually their heads contacted the *Lfa* venom during their attacks. The *Lfa* venom was attractive to the *Pd* majors and minors even when smeared on a glass rod, but was fatal when applied topically. Venomed *Pd* majors were aggressive, attacking their own workers, yet they immediately retreated, bit soil particles, passed their antennae several times through their mandibles, licked the venomed cuticle of their bodies, and followed any moving *Lfa* worker, biting its appendages immediately and holding onto them until the *Pd* worker died. The *Lfa* worker thus attacked spent most of its time attempting to dislodge the dead *Pd* from its appendage. It was also attacked by other majors of *Pd* at the cervix or petiolar region and stung. This *Lfa* worker died within 16 minutes. The *Pd* venom was not always fatal to the *Lfa* workers. They showed extensive antennal grooming and moved in circles

for about 1.4 seconds, following which they apparently recovered. During a 2 hr confrontation, 18 majors and 4 minors of *Pd* were topically venomed and died. *Pd* minors were not as aggressive as the majors. They either held onto the *Lfa* appendages or were grasped at their cervices by invading *Lfa* majors and made end eventually stung. The attack responses shown by the *Pd* majors towards the *Lfa* as compared with responses by *Pd* minors during 20 minutes of confrontation are summarized in Table 2.

The ratio of minors to majors varied from 16.9:1 to 20.1 in the *Pd* colonies. *Pd* majors were isolated from 3 colonies and the *Lfa* response tested. The *Pd* colonies devoid of majors were subdued within 4.2-5 hours as opposed to 7-16 hours when the majors were present.

The *Lfa* workers did not attack during the initial confrontation period but flexed their gasters. On the other hand, the *Pd* majors attacked repeatedly with their mandibles. Most of these attacks were directed toward the *Lfa* appendages and gaster, and only 6 out of 300 (2%) were directed toward the *Lfa* head. When the attacks were toward the *Lfa* head, the *Lfa* worker moved its antennae straight upwards and held them motionless. The next response was for the *Lfa* and the *Pd* workers to grasp mandibles. The *Lfa* worker curled its gaster beneath its thorax and stung the ventrum of the head of the *Pd*. The venomed *Pd* worker was turned loose by the *Lfa* although the *Pd* sometimes held onto the *Lfa* mandibles until death. The *Pd* minors showed attraction to the *Lfa* venom and licked it, but were soon killed. The action was seen to keep the invading *Lfa* out of the *Pd* entrence hole since the *Lfa* were grasped at their stings and pulled out by the *Pd* minors. The minors thus venomed died within 5 minutes.

When all the majors were killed, 2 *Pd* colonies showed a swarming response. The minors and generals held the larvae, pupae, and eggs in

Table 2. Attack responses shown by *Pheidole dentata* majors and minors towards *Solenopsis invicta* workers during 20 min of confrontation (5 replications, n = 100)

Worker caste	Frequency of responses			
	Total	Range	Mean	S.D.
Major	306	38-88	61.2	19.23
Minor	71	9-17	14.2	3.27

Significant ($P = 0.05$)

Seizing, severing, and stinging responses elicited by *P. dentata* workers in the presence of *S. invicta* workers were counted (vide section on *Crematogaster atkinsoni*).

their mandibles and stayed in the entrance tunnel. Three *Pd* workers "scouted" and searched for a secure area. As soon as they entered, they antennated many workers in the nest and were followed by them. The *Lfa* workers were aggressive toward the swarming *Pd* workers. They attacked the mandibles of the queen and stung her. The *Pd* colonies that showed no swarming response were invaded by the *Lfa*, which dug many of their tunnels in such a way as to close a portion of the queen chamber. The *Pd* tunnels were narrower than those of the *Lfa* and were adapted for the colony survival. In nature, such a buried *Pd* colony can be expected to show a delayed escape response. However, in the laboratory the colony was eventually dug out by the *Lfa* workers after 3 days and the brood and queen were transported for food.

Appeasement response

The brood and queen chamber of the *Pd* nest were inhabited by several majors and a few minors whose gasters were distended with liquid food (repletes). These workers migrated to the tunnel leading to the brood chamber and stayed still holding their antennae in repose. Any aggressive *Lfa* worker was met by an akinetic response and slight raising of the head, wide opening of the mandibles and regurgitation of a droplet of food between them. As soon as any aggressive *Lfa* worker opened its mandibles for attack, the *Pd* worker (donor) atennated it at its antennal flagella and then its head while offering the food. The *Lfa* was seen to accept the food and showed no attack response after the food was offered. This appeasement behavior delayed the *Lfa* invasion for 20-30 minutes. Also, the eventual struggle between the *Lfa* and the donor *Pd* workers destroyed some of the tunnels closing off the queen chamber, an additional protection. Appeasement response can be expected to protect the foraging *Pd*

workers from attacks by the extirpator species such as the *Lfa* and reduce competition.

Confrontation index

The confrontation index was tested for *Pd* majors separately, and together with *Pd* minors. When only *Pd* majors were confronted, the index was 351 *Pd* majors to 150 *Lfa*, i.e., 3.34. The index was more if *Pd* majors were mixed with minors in the proportion of 1 major to 16 minors and exposed to the *Lfa* workers for 24 hours. It was seen that 373 *Lfa* were killed as opposed to 1507 of the *P. dentata*; the index was 4.04.

Pheidole morrisi Forel

Habitat:

P. morrisi is orangish yellow ant found in cultivated and fallow fields, as well as open mesophyllic and pine barren ecosystems. This terrestrial species builds triangular, peripherally raised, flat mounds on one side of the nest opening. The mounds are wider, equilateral triangles as opposed to raised equibilateral triangles of *P. dentata*. Three times *P. morrisi* was found nesting in termite-infested hardwood logs. Polymorphism in this species is similar to *P. dentata*, i.e. there are two major forms and one minor form. A *P. morrisi* colony consisted of 200-1000 workers and one queen. *P. morrisi* was seldom found nesting near *P. dentata*.

Colony defense

Colonies of *P. morrisi* (*Pm*) consisting of about 800 workers were exposed to the *Lfa* colonies of similar size. Colony defense of *Pm* was very similar to *P. dentata* described earlier. As soon as the passage

between the colonies was opened, the *Lfa* minors laid a recruitment trail to within 0 5 cm of the *Pm* nest and a trail of 7 *Lfa* minors followed. The foraging *Pm* minors apparently sensed the presence of invading *Lfa* workers. The *Pm* stopped forward movement, slowly waved their antennae and approached the *Lfa* workers. They groomed their antennal flagella, and foretarsi as they came within 3 cm of the *Lfa* workers, opened their mandibles and touched their antennae to the apical club portion of the *Lfa* antennae. The *Pm* minors retreated slightly and again moved forward so as to attack the frontal portion of the *Lfa*. The *Lfa* responded by flexing its gaster and oozing venom at the sting. While 6 minor *Pm* were seen to clasp the *Lfa* mandibles, one returned immediately to the nest its aggressive communication involved antennation with the nest-mates, mandibular, tibial, or cervical contact with the nest-mates. The majors were the first to get stimulated and to come out of the nest. They were seen to approach the *Lfa* workers, and bite off their tibiae and tarsi They continued attacking the *Lfa* workers until all of the appendages were severed. Within 30 minutes a second group of *Lfa* entered the *Pm* nest area.

The *Pm* minors showed ASA response if more than 4 *Lfa* approached any of them. The *Lfa* workers would open their mandibles and bite them. The *Pm* minors held their antennae in repose and stayed motionless. Also, the *Lfa* venom was attractive to the *Pm* minors and it was licked by them when it oozed at the *Lfa* stings. The venom licked by the *Pm* workers induced head-tossing behavior and crippled locomotion. Topical application of the same venom caused the *Pm* majors to attack not only soil particles, but their own workers and those of the alien species repeatedly. Like *P. dentata*, *Pm* majors were more aggressive and showed more attack responses toward the *Lfa* workers than *Pm* minors (Table 3). The venomed *Pm* minors

Table 3. Attack responses shown by *Pheidole morrisi* majors and minors towards *Solenopsis invicta* workers during 20 min of confrontation (5 replications, n = 100)

Worker caste	Frequency of responses			
	Total	Range	Mean	S.D.
Major	218	36-53	43.2	7.63
Minor	86	7-29	17.2	9.12

Significant (P = 0.05)

Student-t calculated from Tables 2 and 3 showed that the majors of *P. dentata* and *P. morrisi* elicited significantly different responses (P = 0.1) while the minors of these species did not.

crawled underneath the *Lfa* majors and grasped their femurs. The *Pm* minors held onto the *Lfa* femurs until death. The attack responses of such *Lfa* workers towards other *Pm* workers were reduced. The majors and minors of *Pm* died within 3-3 2 minutes when they were either stung by the *Lfa* workers or brushed against the *Lfa* venom. The *Pm* workers that received the *Lfa* venom topically followed the *Lfa* workers and attacked them. The *Pm* workers also grasped the *Lfa* mandibles and pulled them. In all cases when *Lfa* released their mandibles, the *Pm* workers were paralyzed for 3-10 seconds, but then recovered. Both species held their antennae upwards during the mandibular attacks.

The *Pm* workers lifted their immatures and moved them into the lower cell. A group of 3 miners was seen to scout a site and return to the brood chamber. A swarming response was shown by the nest-mates. The swarming ants were immediately trailed by the *Lfa* and attacked with the mandibles first and then stung. The stung *Pm* workers dropped the brood and made circular movements, touching their antennae to the ground. The queen did not escape during this swarm. The *Lfa* workers attacked the dead *Pm* cutting them in half, picked up the immatures and carried them into the *Lfa* nest.

The *Lfa* workers entered the *Pm* nest to the deepest cells (see the description for *Pi dentata*) due to the wide and less complex tunnels. They attacked all the *Pm* minors and majors inside the tunnels and received food from the replete major *Pm* as an appeasement response. When food exchange was stopped, the *Lfa* workers attacked and stung the gaster of the *Pm* major. The queen and remaining workers were agitated and left the deeper cells to swarm. The queen was followed by 10 workers, 2 of them crawling over her body. The *Lfa* media were aggressive towards the queen and attacked

the guarding workers fiercely. They then attacked the petiole of the queen, cutting it. Her gastar was carried to the *Sg* nest by a group of *Sg* media. The *Sg* workers were seen to dig out the *Sm* tunnels and destroy the nest structure. The whole *Sm* colony was subdued within 3.15-4.00 hours.

Confrontation Index:

The major *Sm* were exposed to *Sg* and their mortality was 1140 against 500 of the *Sg* (C.I. = 2.28). However, when the majors were mixed with miners in the proportion of 1 *Sm* major to 16 *Sm* miners, the confrontation index was 259 *Sg* to 994 *Sm*, *i.e.*, 3.97:1.

Solenopsis geminata (Fabricius)

Habitat.

S. geminata, the fire ant, commonly inhabits pastures, cultivated and fallow fields, ecotones of agroecosystems and mesic hammocks, pine woods, and open areas in the hardwood hammocks. At Tall Timbers the species was especially abundant in annual burn areas. *S. geminata* mounds are comparatively smaller than the largest *S. invicta* mounds, usually being 30-50 cm wide and 15-20 cm high. There is no discernible opening and the ants were seen to make underground foraging tunnels about 1-3 cm deep around the tumulus of the mound. The colonies were commonly polygynous and contained over 20,000-40,000 polymorphic workers.

Colony defense:

The colonies containing about 5000 workers were connected to the imported fire ant colonies of similar size. When the passage between the two species was opened, the *S. geminata* (*Sg*) workers and *S. invicta* (*Si*)

workers confronted each other in the food dish of the confrontation apparatus. Miners and majors confronted at the same time, but majors showed a distinct pattern of aggressive interactions which the miners followed. The *L. fla.* majors waved their antennae, oriented themselves to the *Sg* majors, opened their mandibles, the same reaction was followed by the *Sg* majors and media. They approached each other and mandibular seizures were immediately exhibited by both species. The *Sg* majors apparently had loose grips due to their worn down mandibles. The *L. fla.* mandibles held onto the *Sg* mandibles for 10-30 minutes. Both species secreted venom drops at their stings and brushed the stings on the other species' sternites, sometimes piercing the intersternal membrane. The venom effect was shown more quickly (0.5-1.2 min) by the *Sg* majors than by the *L. fla.* majors. The *Sg* majors curled their gasters, appendages, straightened their antennae, and held their mandibles fast on those of the *L. fla.* majors. The *Sg* workers were released from the *L. fla.* mandibles later. In 32% of the cases, *L. lo.* majors responded to *Sg* stings. The *L. fla.* waved their antennae, stretched and curled their legs, and released their mandibular grasps. However, only 23.4% of the pairs curled their abdomens and died within 15 minutes. The *Sg* venom and the alarm and defensa releasers from the *L. fla.* venom apparently transmitted the aggressive reaction among surrounding *L. lo.* workers. Even the *L. lo.* workers 4 cm from the attacking pair opened their mandibles and oriented in that direction. A frequent antennation was seen among the workers coming from the colony and the workers once involved in attacks in the area of confrontation. The miners and media touched their flagella to those of their nest-mates 3-4 times, groomed their antennae and opened their mandibles. Within 10 minutes a large file of workers from both the *L. fla.* and the *Sg* colonies confronted

in the feeding dish. The mandibular grasps were now as frequent as the grasps at the petiole, legs and antennae. Also, the attacks between majors, miners and media were independent of the size of the attacking members. Two or more miners held onto the mandibles, some of the appendages and the petiole of a single *L.f.a* major (Fig. 6). The grasps at the cervix ended in cutting the heads from the rest of the bodies. The frequency of attacks at different body parts of the *Sg* exhibited by the *L.f.o* workers is shown in Table 4.

The *Sg* workers laid down a substrate of soil particles in the glass tube connecting their nest to the food dish. Such provision was also seen in their foraging tunnels. The invading *L.f.o* majors walked through the tunnels only with difficulty. The *L.f.a* workers were trapped between the guarding *Sg* workers and the workers in the foraging tube. The influx of a large number of *Sg* workers from the *Sg* colony stimulated the invaders to turn back, but they were frequently antennated by the *L.f.a* miners at their gasters and were "forced" to move forward. Gaster-flexing and venom-secreting response was immediately attained by the trapped *L.f.o* workers (Fig. 7, top). The vaporizing *L.f.a* venom caused grooming in the *Sg* workers. The *L.f.a* workers made their way through the grooming *Sg* workers since a comparatively lesser number of attack responses (3.5%) occurred in the tube. A second exodus of *L.f.a* invaders pushed the *Sg* workers in the tube to the *Sg* nest and killed them. Also, soil substrate in the tube was cleared by the entering *L.f.o* workers by pushing the soil particles with their front and hind legs. Similar "digging" response was continued by the *L.f.o* workers on reaching the *Sg* nest. Severe confrontations were observed between the digging workers and the *Sg* workers guarding the nest. While over 50% of the *L.f.o* workers (mostly miners) were

Table 4. Frequency of mandibular attacks exhibited by *Solenopsis invicta* workers towards *Solenopsis geminata* workers within 5 min of confrontation (5 replications, n = 100).

Worker caste	Portion attacked			
	Antennae	Mandibles	Legs	Gaster & petiole
Major vs major	17.3	6.0	27.1	3.4
Major vs minor	19.2	11.3	8.2	5.0
Minor vs minor	7.3	8.6	11.2	11.4

Figure 6 Attack responses of *S. invicta* towards *S. geminata*.

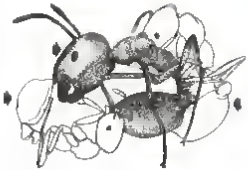
Gaster-flexing posture exhibited by a *S. invicta* worker in the presence of *S. geminata* workers. Antennae are slowly moved and a venom droplet is secreted at the tip of the sting by the *S. invicta* worker during this response (Top).

Two *S. invicta* minors seizing the appendages of a *S. geminata* major (stippled), and stinging its head and gaster. Antennae are held upwards by the seized *S. geminata* worker (Bottom, left).

Two *S. invicta* minors seizing the antenna and mandible of a *S. geminata* major and stinging its alitrunk (Bottom, right).

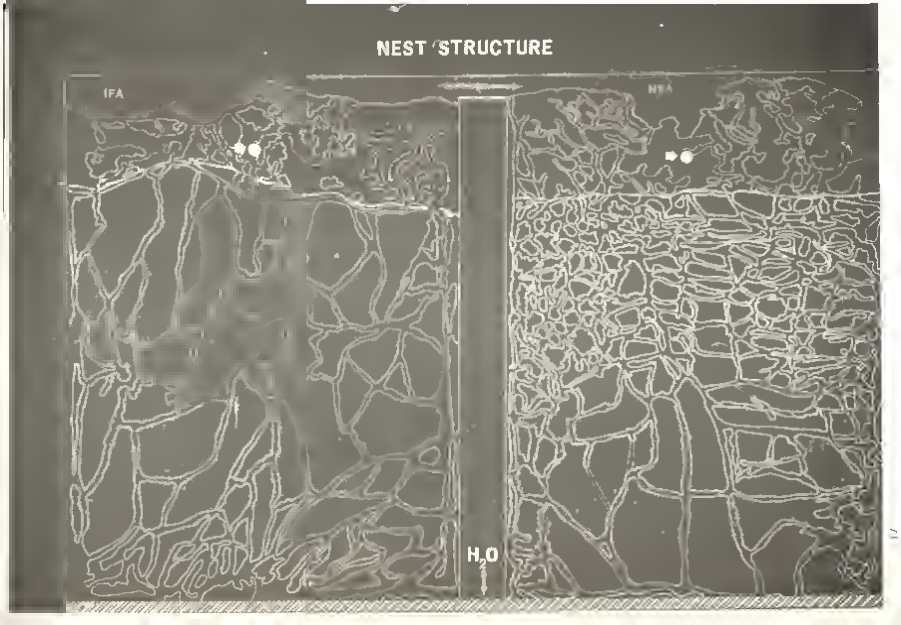
1

1 mm



1 mm

Figure 7. Comparison of the nest building tendency of *S. invicta* and *S. geminata* in a vertical plane. Vertical tunnels made by *S. invicta* (*Si*) are widely spaced and connected with oblique tunnels. Those made by *S. geminata* (*Sg*) are closely spaced and connected with numerous horizontal tunnels. The nest structure of *S. geminata* protected its colony against the *S. invicta* invasion. (Arrows show holes for introducing ants via glass tubing. Depth of the nest is 30 cm.)


NEST STRUCTURE
IFA
NFA
H2O

excavating new tunnels, the others (mostly media and majors) were killing the *Sg* workers. High mortality of both species was observed during these assaults. The whole *Sg* colony became agitated and the brood and the queens were moved deeper in the nest. The upper part of the *Sg* colony was full of aggressive *Sg* majors, minors and media.

Comparative study of the *Lfa* and *Sg* nest architectures demonstrated the protective provisioning in the *Sg* nest. The tumulus and the upper 10 cm area of the *Sg* nest consisted of 3-4 mm wide horizontal tunnels, interconnected with oblique tunnels, forming a reticulation of 3-4 cells per 4 cm^2 of the vertical nesting area. The *Lfa* nest, on the contrary, consisted of wider (4-5 mm) vertical tunnels, interconnected to form 1.3 cells per 4 cm^2 area (Fig. 7). The invading *Lfa* workers excavated tunnels vertically downwards, widening them sometimes by holding a quartz particle in their mandibles and moving it along the sides of the tunnel. The *Lfa* workers behind the excavating workers removed the soil particles to the outside of the nest. The rate of tunnel widening was 2-3 mm per 10-15 seconds. In effect, many *Sg* tunnels were blocked, trapping the workers inside. They were killed during the next 24 hours. The callows and the *Sg* queens were comparatively passive to the attack. The queens of *Sg* bit the attacking *Lfa* workers and repelled them, some physiochemical activity was apparent. However, the massive attacks at the queen's petiole severed it from the rest of the body. The brood and the gasters of the *Sg* queen were used as food by the *Lfa*. The *Sg* nest was used as a storage area by the *Lfa* for 7-10 days but was soon abandoned.

The *Lfa* venom was fatal to the *Sg* workers, applied topically or subcutaneously, the mortality was seen within 6-20 minutes. The *Sg* venom was also fatal to *Lfa*, but its effect was slow (30-50 min). In

low concentrations, venom of both species stimulated alarm behavior, and in high concentrations, attack behavior. Also, the *Sg* venom stimulated aggressive attempts in the *Afa* workers, but the *Afa* venom, in high concentrations, was apparently repellent to the *Sg* workers and provoked social grooming. The alarm defense system was effective during the colony aggression described above.

Confrontation index

The majors of *Sg* were kept captive by letting the minors and media pass through a 2 mm glass tubing. These workers were used for C.I. studies. It was seen that 382 *Sg* majors were killed against 76 majors of *Afa* (1 *Afa* to 5 *Sg*). However, the C.I. of polymorphic populations was 1.88, showing increased attack responses by *Sg* media and minors.

Solenopsis pergandei Forel

Habitat:

S. pergandei was generally found nesting in cultivated and fallow fields, partially shaded areas in pine woods, mowed lawns, and roadsides. This tiny monomorphic species made 10-15 cm mounds of fine loose soil. After rain, the tiny network of galleries in the tumulus appeared like a honey comb. The tunnels were 1-3 mm wide. The colony was polygynous with 1000-4000 workers. This species is apparently nocturnal and cryptic in habit.

Colony defense

The mound of *S. pergandei* (*Sp*) is without any discernible entrance hole. When a colony of this species was connected to one of *Afa*, the foraging workers of *Afa* showed no aggressive behavior until they encoun-

tared foraging *Sp* workers at 6:00 p.m. The *Sp* workers easily passed under the *Lfa* workers and showed no movement until the *Lfa* workers moved away. The escaping *Sp* workers entered their nest immediately. The *Lfa* workers followed the *Sp* workers and excavated their mound. About 30 *Sp* workers were seen to crawl out and bite at the appendages of the excavating *Lfa* minors and media. No attacking behavior was shown by the *Lfa* workers. However, when *Sp* workers crawled up to the gaster of the *Lfa* and stung it or held onto the *Lfa* antennae with their mandibles, the *Lfa* workers ceased excavation, opened their mandibles, and showed an intensive grooming reaction. The grooming was momentary (0.5-1.0 min) and was followed by an increased biting response. Even the small soil crumbs were bitten. The *Lfa* workers moved in a circular fashion while attacking.

The *Sp* workers are 1/3-1/2 the size of the *Lfa* minors and about 1/2 as narrow. Any mandibular bite by the *Lfa* provoked a gaster-raising posture similar to that by the *Lfa* workers. The *Sp* workers secreted venom at the tips of their stings, however, no abdominal flexing was apparent. The biting *Lfa* passed its mandibles over the alitrunk and the raised gaster of the *Sp* worker. The action was facilitated by the movement of the *Sp* under the *Lfa* body. The *Lfa* worker was seen to jerk immediately, open and close its mandibles, but showed no attack of any sort for 3-3.5 seconds. It rubbed its mouthparts on soil, biting the soil particles, and intermittently passed its antennae through the mandibles. The reaction spread the venom on the antennae, which curled abnormally within 2-3 minutes. Such an *Lfa* worker was aggressive to the *Sp* workers and followed them, biting several times at their dorsum and cutting them into pieces. Stinging response was not shown by the *Lfa*

worker. The *Lfa* mortality was slow since the venomed *Lfa* recovered after 20 minutes. However, the venom reaction disabled its antennae. While some *Lfa* workers (about 1/3 of the invaders) attacked the *Sg* workers, a large number continued excavation of the *Sg* nest for over 8 hours. The alates and queen *Sg* were passive. The *Sg* workers dispersed all around the mound and attacked the intruders. Their attack responses were reduced when 50-5% of them were bitten and severed. Outnumbering *Lfa* workers subdued the *Sg* colony after 8-12 hours. Intricate colony structure protected part of the *Sg* colony. In 5 experiments, at least one queen and 300-1000 workers were captive in the closed tunnels of the nest, the closing of the tunnels was due to the digging process of the *Lfa* workers. In the laboratory nests, the remnant colony was also attacked after a period of 2-3 days, but in the field it may escape attack. *Lfa* majors did not take part in the confrontation. Cryptic nest structure protected the *Sg* colony in spite of the minute size of the workers and low colony size. However, colonies of *Sg* were not seen near the *Lfa* colony in the field.

Confrontation Index

In a series of experiments, 1020 *Sg* workers were killed and the mortality of *Lfa* was very low (17 workers). The C.I. was therefore 60.00.

Pogonomyrmex badius (Latreille)

Habitat

Pogonomyrmex badius, the Florida harvester ant, is common to pine barren, turkey oak association, and other semi-dry, sunny, open and sandy areas in Florida. It is a comparatively xerophilous species at

Tall Timbers and its occurrence is limited to burnt areas. *P. badius* is a granivorous species although it was also found feeding on living and dead arthropods. This is the only polymorphic North American species of this genus (Kusnezov 1951). It builds flat, 20-30 cm mounds with rounded edges and a large 1 cm entrance hole. On the average, colony size varies from a few hundred to 2500 individuals with one fertile queen.

Colony defense

A colony of 1000 Florida harvester ant workers, a queen and several alates was reared in a rectangular plastic nest and was connected to a normal sized *S. invicta* colony reared in a Wilson cell. The passage between the colonies was opened. The *Sa* minors made a recruitment trail within 10 minutes and one *Sa* minor encountered a seed-carrying *P. badius* (Pb) worker. The *Pb* worker stopped, dropped the seed, opened its mandibles, raised its thorax, head and legs, curled its gaster beneath its legs parallel to the ground, and made a 2 cm circle around the *Sa* worker. The *Sa* worker lowered its head, held its legs apart, opened its mandibles, and exhibited gaster-flexing posture. Within 0.3 seconds a tiny droplet of venom was seen at the tip of its sting. It turned its head to the direction of the harvester ant worker, and slowly waved its antennae. The circling harvester ant increased the frequency of circling. This was apparently a reaction to the *Sa* venom. When the *Sa* was removed, the circling movements began to diminish within 1-30 minutes. The circling ant encountered its nest-mates, they moved towards the *Sa*, and were stimulated to encircle the *Sa* worker with a series of loops. The alarm-carrying *Pb* workers entered their nest and waves of alarm were disseminated throughout the colony. The *Sa* worker resumed locomotive posture and oriented itself towards its nest. It encountered other exploring *Sa*

media and minors, stroked their antennal flagella 3-4 times and reached its nest. All the *Af* workers encountered moved towards the *Pb* colony and started exhibiting gester-flexing. The whole *Af* colony was agitated More and more majors (13) were recruited along the fast-moving *Af* trail.

Within 15 minutes of confrontation, more than 100 minors, media and 22 majors of *Pb* poured out of the nest, all of them curling their abdomens beneath their thorax as soon as they reached the nest entrance. The gester-flexing *Af* workers slowly moved towards the nest entrance (point of maximum alarm stimulus), and within 20 minutes 3 majors and 16 media and minors were seen to flex their abdomens in an area of 3-4 cm diameter around the 0.5 cm diameter nest entrance. The *Pb* workers on the nest surface bit the *Af* gesters and appendages and swiftly moved away. Biting crushed the portions attacked but did not cut them. In only 3 cases did the *Pb* workers sting the *Af* majors. In these cases, they held the *Af* legs between their mandibles. *Af* workers so attacked made crippled movements and bit soil particles. They recovered within 30-35 minutes. However, the *Af* workers attacked by majors, media, and minors of *Pb*, bled and died within 1.5-2 hours. The *Pb* workers smeared with the *Af* venom alternately thrust their forelegs into the soil in a digging motion. They continued digging up to 6-10 minutes, then fell on their side and stretched their appendages. They opened their mandibles and curled their abdomens before they died. Such dead ants were carried by other *Pb* minors and were dropped away from the nest entrance. About 7.2% of the *Pb* workers on the nest surface attempted to crawl up the nest walls (escape response).

Near the *Pb* nest entrance, the *Af* flexed their abdomens and were pulled away from it by *Pb* workers. Two *Pb* majors and 3 minors dug inten-

sively around the nest opening closing it partially within 5 minutes. However, they were attacked by the *Lfa* at their legs and were stung before the nest was completely closed. The *Pb* workers near the nest entrance and those buried in the nest showed continuous gaster-flexing movement (stridulation) and digging. Digging behavior was now exhibited by the *Lfa* workers. They opened the nest entrance and attacked the *Pb* individuals. Some *Pb* workers moved to the queen and brood chambers, and started moving the brood into lower chambers. However, the queen and some generals transported the brood towards the nest entrance. They were easily attacked by the *Lfa* workers. The *Pb* queen attempted to attack with both her mandibles and sting, she killed 3 *Lfa* minors. She was venomed and showed crippled movement similar to workers of her own species and died. The alatae held their antennae upwards, attempted no aggressiveness, and moved fast as soon as any *Lfa* workers climbed on them and bit their wings. They avoided stings for about 10 minutes, but did not escape from the nest even though they reached the nest entrance.

The *Lfa* traffic to the *Pb* nest increased. The *Lfa* inside the *Pb* colony transported all the dead and brood out of the nest, but carried only the brood to their nest.

Confrontation index

Two hundred individuals, irrespective of worker size, were exposed during confrontation tests. During 4 replicates, 482 *P. badius* workers were killed as opposed to 144 of *S. invicta*. The confrontation index was 3.34. Circling and looping were shown by the *P. badius* workers during the initial 3 minutes and then digging responses were observed. Also, gaster-flexing (stridulating) *P. badius* workers made a multidirectional movement encountering many *Lfa* workers, and were eventually killed.

Tribe: Attini

Cyphomyrmex rimosus minutus Mayr

Habitat:

C. rimosus minutus is a fungus-growing species inhabiting open mesophyllic hammocks, pine woods and fallow fields. This species nests in open ground, in the cavities at the base of oak trees, magnolia trees, under the bark of rotting logs, and in the leaf litter. It is also found nesting near (1-3 meters area) the red imported fire ant and the native fire ant and grows fungus on the dead, discarded fire ants, insect parts, and fecal pellets of lepidopterous larvae. A pile of pellets is left near the nest opening of the sloping 6-10 cm mound.

Colony defense:

Colonies containing about 1000 ants were exposed to the *Lfa* colonies (1500 individuals). The *Lfa* workers moved randomly and then entered the *C. rimosus minutus* (*Cr*) nest opening. The guarding *Cr* worker held its antennae close to the vertex following the antennal touch by an intruder. The *Lfa* workers came out of the *Cr* nest and moved at random. The *Cr* guard crawled over the nearest sister worker which shook its own body vigorously, an aggressive message transfer. Similar behavior was repeated by the second ant to the third and a few more (about 6-10). The *Cr* workers again foraged around and the colony was not agitated. When another *Lfa* worker, a minor, reentered the *Cr* nest, the guard *Cr* opened its mandibles, shook its body to and fro, but held its legs stationary. The *Lfa* worker went out in response to the distress signalling. The *Cr* guard turned and antennated 3-4 times with its nest-mates. A group of *Cr* workers stayed near the entrance following the *Lfa* invasion. During the third invasion by a

single *Lfa* worker, the guarding workers retracted their antennae into the antennal scrobes, opened their mandibles, and jerked their abdomens or their entire bodies 11-13 times until the *Lfa* moved out. During a 20 minute period, the workers inside the nest moved the brood, queen, and the fungal pellets to the innermost part of the nest cavity. During the fourth invasion, the *Lfa* were again "distressed," but they moved freely through the *Cx* nest. Following the increased number of encounters between the guarding *Cx* workers and the invading *Lfa* workers, the distress response decreased and the *Cx* workers elicited ASA response. Each worker held its antennae in the antennal scrobes protecting them from any mandibular attack, curled its head ventrally, brought its legs close to the ventrum and curled its gaster, touching the hind tibiae. The ant appeared like a tiny ball with some sticks protruding out (Fig. 3; 3 and *Cx*). The response was intensified when the *Lfa* biter crawled over the *Cx* worker. Microscopic observation showed that the *Cx* cuticle has numerous silvery setae (sensors) along the frons, clypeus, vertex and dorsal portion of the antennal scapes. Similar sensors are dispersed in approximate rows on the elevated areas of the humeral angles of the promesonotum (3 in number), slightly smaller areas on the mesonotum (2 in number), and epinotum along the declivious face. The sensors are oriented and concentrated towards the apex of the elevated areas of the alitrunk. The dorsal petiolar, postpetiolar, and gastric regions possessed the sensory patches. Mechanical stimulation of the sensory patches triggered the ASA response in *Cx* workers (Table 5).

Stimulation of antennal scapes and the frontal areas created temporary prolongation of the ASA response, as compared to the stimulation of the thoracic and abdominal sensory areas where the delay in mobility was over

Table 5 Relation of mechanical stimulation (teasing with forceps) of different sensory areas on the persistance of aggression-suppression-akinesis (ASA) response in *Cyphonaynnex numesus minutus* (5 replications)

Sensory areas	Response time (seconds)	
	Range	Mean
Antennae + frontal area	3.0-32.8	14.1
Frontal area, left antenna amputated	60.8-96.4	83.9
Frontal area, both antennae amputated	14.3-30.2	22.52
Dorsum of pronotothorax	102.0-331.0	186.52
Dorsum of postpetiole + 1st gastric segment	152.0-205.0	185.58

3 minutes. The *L.f.a* workers did not create such a prolonged delay since the mechanical stimulus has always been too intense (Table 6). Also, a short period ASA response by *C.t.* workers increased their protection in addition to their escaping from the site of the disturbance following the ASA response.

The *C.t.* workers responded for a shorter period if disturbed by the *L.f.a.* workers only once than when disturbed from 2-5 times. If the frequency of disturbances was more than five, the ASA response was prolonged for over 10-26 seconds.

The *L.f.a.* workers removed fecal pellets and dead insects from the *C.t.* nest opening (17 cases) without much resistance, one *C.t.* worker pulled a dead insect from the *L.f.a.* mandibles. After 2 hours, one third of the *C.t.* colony moved out of the nest as an escape response. The *C.t.* workers reentered the nest and carried the fecal pellets and fungal mat, but were attacked by the *L.f.a.* workers now occupying their nest. The heads of the *C.t.* workers were cut off. The *C.t.* colony in the deeper part of the nest made no attack. After 22 hours, the queen moved deeper into the nest. During 13 out of 125 cases, the *C.t.* individuals moved their legs while in the *L.f.a.* mandibles, and the rest displayed ASA response. Half of the nesting area was occupied by the *L.f.a.* and the other half by the remaining *C.t.* colony. One third of the workers thrown out returned into the nest and moved freely through the *L.f.a.* workers. However, the expulsion behavior seemed to be continuous since the whole colony was expelled after 32 hours. The *C.t.* brood was not taken to the *L.f.a.* nest by the *L.f.a.* The *L.f.a.* workers exhibited mandibular attacks at the antennae, cervix, thorax and petiole, cutting the heads and gasters. In one case, 252 *L.f.a.* occupied the *C.t.* nest within 48 hours, throwing 153 ants out; 15 were severed at

Table 6. Relation of disturbance by the *Solenopsis Invicta* workers to the persistance of ASA response in *Cyphomyrmex rimosus minutus* workers.

Number of times disturbed (antennated, crawled over, bitten)	Persistance of ASA response (seconds)		Cases
	Range	Mean	
1	0.5-8.4	3.35	26
2	4.0-17.8	8.43	11
3	4.0-13.2	7.02	12
4	4.2-13.2	8.83	7
5	4.5-9.1	6.14	7
6	10.2-26.0	19.15	6

their heads and abdomens. Mere biting responses, without cutting the body parts, elicited ASA response in *Ct* workers. When the cephalic portion was bitten 2-4 times, the response was persistent for 12-20.1 seconds, when the gaster was bitten, it stayed for 8 2-15 seconds, when the legs were bitten it persisted for 8-9.2 seconds; and when the petiolar region was grasped, it persisted for 15.6 seconds. When the mandibles were clutched, the ASA response persisted for 17.2 seconds. If the number of *Lfa* were increased to a ratio of 14 to 1 *Ct* worker, the *Ct* worker opened its mandibles and became aggressive for 2-3 seconds. It was followed by an ASA response again.

The *Ct* worker apparently displayed apasematic coloration and episematic structures, like the pieces of bark, fecal pellets, etc., by retracting its body to minimal possible size. It also possessed a crush-resistant cuticle. A distinctly different trophic level, in addition to the tolerance to the *Lfa* attacks, protected *Ct* from being destroyed. The episematic and ASA responses by *Ct* had been to its advantage since it collected dead *Lfa* from the *Lfa* mound and used it as a substratum to grow fungus. In the laboratory, small colonies of *Ct* and *Lfa* were reared in the same Wilson cell for 3 months.

Due to completely passive defense, no confrontation index could be accurately calculated for *C. nimosus minutus*.

Trachymyrmex septentrionalis (McCook)

Habitat

T. septentrionalis is a second mycetophagous species. It is abundant in open and partially sunny habitats of silviecosystems, fallow and mowed fields, pastures, and fire breaks. The mounds are semicircular, about

20-40 cm diameter, 1-5 cm away from the nest opening. The superficial, hypogaeic brood cells lay underneath the mound. The fungus cells are built at the ends of two of thrice-branched tunnels. Two to three queens are not unusual in a single nest.

Colony defense

Colonies of T. *septentrionalis* (Ts) containing 250 ants were exposed to the *Lfa* colonies (1500 ants). The *Lfa* workers entered the Ts nest area within 20 minutes. The Ts workers were excavating and did not respond to the randomly moving *Lfa* worker. The *Lfa* returned and recruited 11 media and minor workers from its nest. The confrontation behavior between the workers of Ts and *Lfa* was of particular interest. The Ts workers mimic the coloration of the nesting soil. The soil particles they excavated were almost of their own size. Aposematic coloration and structure were speculated for the lack of aggression by the *Lfa* workers for the first 22-30 minutes. The Ts workers approached each other, placed their antennal tips on the antennae of each other, then touched their foretibiae and stayed near each other in a group. The *Lfa* workers (3 media and 5 miners) antennated the Ts and crawled over them 8 times. The Ts workers displayed ASA response for several minutes and moved after the *Lfa* workers left. The phenomenon was explored in detail. Whenever the *Lfa* worker antennated or showed mandibular attack, the antenna touched was brought in repose in the well developed scrobe by the Ts worker (Fig. 3, Ts). If the *Lfa* stimulus continued, the next antenna was retracted and only the foretibiae of the Ts worker made a slow to and fro movement. The *Lfa* worker ceased antennation and crawled over the Ts. The Ts worker jerked its body three times, retracted its legs, and stayed motionless. The *Lfa* worker returned, antennated the Ts worker caudad when again the Ts worker jerked 3 times as

a distress signal. The *Lfa* worker again crawled over the *Ta* worker and it made a slow movement of the hind legs, the other portions of the body were held motionless. The *Lfa* worker continued crawling for about 10 times and the *Ta* worker stayed immobile (Fig. 3, 2). It moved the fore leg of one side and the middle and hind leg of the other to crawl forward with its antennae still in repose. During the 11th and the following crawling, it moved faster and dragged its body with the *Lfa* worker riding on its alitrunk. Due to the fast motion, the *Lfa* worker dropped. The *Ta* worker showed aggressiveness by opening its mandibles, waving its antennae, and holding the normal locomotive posture. A similar posture was held for 1 hour if the *Lfa* worker attacked at the jaws or legs. The *Ta* workers also secreted a nonviscous liquid which spread along their mandibular grooves, antennal carinae, and the whole face due to the surface tension provided by the rugose facial area. Simultaneously, a yellowish secretion was spreading from the anal area all along the abdominal rugosity. The secretions were not repulsive to the fire ants since 3 *Lfa* workers balled around the *Ta* worker, bit its head, alitrunk, and abdomen, and followed by stinging. The *Ta* secretion may facilitate the spread of the *Lfa* venom over a larger portion of the cuticle, and the intersegmental membrane. The secretions were not attractive to the *Lfa*. Apparently, the *Lfa* venom was slow acting since the *Ta* worker died only after 1.5-2 hours of attack. The clustering *Ta* workers grasped the antennae, gasters, and legs of the attacking fire ants. Their serrated mandibles slid over the *Lfa* cuticle with sore cuticular injury to the antennae and legs. None of the portions were severed. The *Ta* workers attacked and moved away quickly.

The *Lfa* workers held the *Ta* cervix for 3-7 minutes, severing it from

the rest of the body. The numerical force of the *Lft* increased to 56 workers within the next 20 minutes. They held the jaws, the well developed antennal carinae, and the gasters of the *Ts* workers between their mandibles for 3-5 minutes and left. The *Ts* workers kept their mandibles closed, but when opened after 2-35 minutes, the *Lft* near them were attacked immediately, showing that the mandibular secretion elicited aggression (43 cases). When the number of *Lft* workers increased to the proportion of 1:16 or 5:40, the *Ts* workers again showed delayed immobility and escape behavior. The proportion of *Lft* workers was increased from 1-5 in a series of experiments. The responses shown by both species are summarized in Table 7.

The *Lft* workers invaded the *Ts* colony and attacked the queen and callows and removed the fungal mat outside the chambers. None of the *Ts* workers were taken to the *Lft* colony and the complete *Ts* colony was not killed even after 36 hours. The hard and rugose cuticle, ASA response, and eposematic coloration protected the *Ts* colony from complete destruction for a prolonged period. The 2 species were seen to nest in a vicinity of 3 meters from each other and are on distinctly different trophic levels. The *Lft* is carnivorous and the *Ts* fungivorous, growing its fungus on saprophytic substrate like dead insects, larval pellets, etc. The crescent-shaped mound and the hypogeaic nest structure did not impart colony protection. In the laboratory, *Ts* colonies could not be reared with *Lft*, as could the *C. nanosus minutus*.

Confrontation index:

A definite confrontation index could not be computed since the *Ts* workers showed passive defense towards the *Lft* workers. However, *Lft* workers were killed in the proportion of nearly 1 *Lft* to 16 *Ts* (or 2-32 and 10-163) when the number of *Ts* workers was large. The C. I. was

Table 7. Confrontation responses shown by *Trachymyrmex septentrionalis* and *Solenopsis invicta* workers during 1 hour of observation

Trachymyrmex septentrionalis		*Solenopsis invicta*	
Responses	No. of workers	Responses	No. of workers
ASA response	1	Locomotion	1
Antennae close to face & jerking	5	Mandibular attack	1
Above & mandibles open	7	Retreat & escape	1
Mandibles open	16	Escape	1
Followed *Lfa* & attack	28-42	Escape	1
Same as above	50	Gaster-flexing & venom secretion	1
Mandibular opening	50	Mandibular opening	2
Attack	50	Same as above	3
ASA response	50	Mandibular attack	4
Antennation of 4 nest-mates & escape	50	Above & stinging	5+

therefore about 16 and over.

Tribe: Crematogasterini

Crematogaster atkinsoni Wheeler

Habitat:

C. atkinsoni is a monomorphic, arboreal species. It was found nesting in the reeds of pithy herbs and shrubs growing along lakeshores, fence rows, and marsh lands. Larger nests of *C. atkinsoni* were collected from *Cephalanthus occidentalis*, *Eupatorium* spp., *Catalpa speciosa*, and *Pinus* spp. The colony size varied from 1300-12,000 workers and a single queen was usually located. In the laboratory, this species nested in horizontal and vertical glass tubing.

Colony defense:

Vertical tube-nests of *C. atkinsoni* (C) containing about 1500 workers were used. When the passage between the *L.f.* colony and C colony was opened, *L.f.* miners laid a recruitment trail up to the nest opening of *C.* At the arrival of the first *L.f.* worker, the C worker waved its antennae slightly while still in the tube, opened its mandibles, and turned its dorsoventrally flattened gaster over its alitrunk so that the flattened petiolar node rested on the epinotum between the spines. The epinotal spines not only anchored the abdomen but also provided protection during any mandibular attacks by the *L.f.* workers.

Definite patterns of alarm-attack and escape responses were followed by arboricolous and some terricolous ant species in the presence of *S. invicta* workers. A scheme of responses is presented below

Response A. random movement, raising head and vibrating antennae (alerting)

Response B orientation towards an alien worker

Response C. antennal contacts between two workers followed by retreat (recognition)

Response D mandibular opening and an associated alerting response by the nearest nest-mate

Response E. seizing mandibles of the alien worker

Response F seizing legs of the alien

Response G: seizing petiole of the alien

Response H seizing cervix of the alien

Response I: pulling and dragging

Response J severing the seized part

Response K: stinging

Response L escape or retreat from the site of attack

These responses can be further grouped into conventional alarm and attack responses:

Alarm responses		Attack responses		
alert	activation	seizing	severing	stinging
A	B C D	E F G H I	J	K

The responses A, B, and C were reduced during the first assault and the response B was prolonged (Table 8). The guarding C worker emerged out of the nest, secreted a vile-smelling poison droplet at its abdominal tip which spread along the spatulate sting. This secretion only repelled the invading *Ma* worker, but induced a mandibular secretion and gaster-

Table 8 Frequency of attack responses shown towards *Solenopsis invicta* by *Crematogaster atkinsoni* and *C. ashmeadi* during 20 min exposure (n = 5)

Responses	*C. atkinsoni*			*C. ashmeadi*		
	Range	Mean	Total	Range	Mean	Total
Alert (D)	3-12	7.0	35	4-9	7.0	36
D + E	5-8	5.6	28	1-7	3.2	16
D + F	6-18	10.2	51	5-9	9.8	39
D + G	0-1	0.2	1	0-1	0.2	1
D + I	8-19	9.2	46	9-10	8.9	44
D + I + J	1-21	7.4	37	1-7	4.2	21
L	0-3	1.2	6	2-7	4.4	22
Total aggressive (alarm & attack) responses		198			155	
% alarm responses		17.63			22.43	
% attack responses		82.82			77.64	

curling behavior in the surrounding C workers (alarm response). A large number of C workers (7-36) poured out of the upper compartment of the C nest. The *L. fuliginosum* worker opened its mandibles and assumed a gaster-flexing position. No mandibular attacks were observed. The C workers reentered their nest and the *L. fuliginosum* worker returned to its colony. After 10 minutes, a file of over 30 *L. fuliginosum* media and minors entered the confrontation tube and crawled over the C nest. The C workers were more aggressive during this attempt since they bit at the appendages of *L. fuliginosum* and held onto them until the assaulting pairs dropped off the nest. The mandibular attacks increased the frequency of C workers being brushed by the *L. fuliginosum* venom. However, the C workers held onto the *L. fuliginosum* appendages until death. The C workers severed the *L. fuliginosum* appendages. Stinging (attack response K) on the part of the C workers was not observed. The guarding ants were replaced by the workers from the lower compartments. The third attack by *L. fuliginosum* workers followed after 30-40 minutes. The invasion was resisted in the same way by guarding C workers. When a continuous file of *L. fuliginosum* workers involving over 200 workers was on the C nest, more C workers emerged from the nest and the attack continued for more than 1 hour. The fourth attack followed after 25-33 minutes. During the time lapse, one guarding C worker was seen to run along the nesting area and reenter the nest. It antennated the nest-mates and the whole colony was agitated. An escape response followed, 72 C workers grouped in small pocket outside the nest. Escape response also occurred after 4-2 hours (mean of 5 colonies), *i.e.*, after the sixth *L. fuliginosum* attack, when 16 1-62.3% of the C workers escaped from the nest (Appendix 4). The workers attached their larvae and egg masses at their spatulate stings and held them in the air above their alitrunks. This novel brood transport of eggs and smaller larvae apparently increased

the speed and safety of transport. Larger larvae and pupae were held between the mandibles and carried. The queen was followed by at least 3-5 C workers and guarded against the *Lfa* workers during eventual *Lfa* attacks under captive conditions. The escape site was accessible to the *Lfa* in the laboratory experiments, but budding of the C colony can be expected under field conditions. The remaining C colony was invaded by the *Lfa* workers. Mandibular attacks and stinging responses were intensified. The callows of C were passive but they did curl their gasters. The gasters of C were not severed during the assault as a result of the protective function of the epinotal spines. Biting responses on the raised petioles of C were seen but were unsuccessful.

Crematogaster atkinsoni built cartons inside the glass tubing only in one case. The invading *Lfa* spent 1-2 hours cutting and nibbling through the carton to reach the queen cell. Thus, carton nests provide protection as well as moisture insulation.

Crematogaster ashmeadi Mayr

Habitat:

C. ashmeadi is a monomorphic, cavity-inhabiting species found in the hollowed stems of *Eupatorium* spp., *Cephalanthus occidentalis*, Sumac, *Vitex* spp., *Smilax* spp., *Quercus* spp., *Magnolia* spp., and *Pinus* spp. It was abundant along the lakeshores and marsh lands. In the laboratory, the species nested in vertical or horizontal glass tubing. Large colonies contained over 3000 workers.

Colony defense:

Large colonies containing about 1500 workers were connected to the *Lfa* colonies of equal numerical strength. The confrontation behavior of

C. ashmeadi (Ca) was very similar to that of *C. athensana* described earlier. However, the frequency of responses (attack responses) was different. The invasive behavior, shown first by the scouting *Af* minor and then by the trail-following media and minor *Af* workers, was also similar. The guarding Ca worker stayed in the tube until the first *Af* worker came near the entrance hole. The guarding Ca worker opened its mandibles, held its gaster over its alitrunk, and secreted a vile, odorous secretion at its abdominal tip. The spatulate sting held the poison droplet and apparently facilitated its diffusion all around the ant's configuration. A group of 22-30 Ca workers in the upper nest compartment exhibited similar behavior within the next 3 minutes. The *Af* worker exhibited gaster-flexing posture, oozed a droplet of venom at the tip of its sting, and stayed still until all the Ca workers re-entered their nest. The whole reaction was completed within 4-3-5 5 minutes. The *Af* worker ran up to its nest, entanneting all the encountered nest-mates. A file of over 55 *Af* workers was seen on the Ca tuba nest. A group of 100-115 Ca workers poured out of the nest and attempted mandibular attacks, pulling appendages and grasping at the *Af* mandibles. Comparative study of the attack responses of *C. athensani* and *C. ashmeadi* showed predominance of appendicular attacks (responses F, I, and J) in *athensana* over *ashmeadi* (Table 8). The epinotal spines of *C. ashmeadi* were shorter than those of *C. athensana*, but they protected the petiole from mandibular attacks by the *Af* workers. The biting *Af* slid its mandibles over the projecting spines and then the petiole. The abdominal secretion of Ca was also repulsive to the *Af* workers for 30 seconds to 2 minutes, but it did not reduce any venom-oozing response in the aggressive *Af* workers. The *Af* venom was toxic

to the *Ca* workers. When brushed with the venom, the *Ca* workers closed their mandibles and curled their legs. The attacked *Ca* workers held onto the *Lfa* appendages until death. The toxin from either *atkinsoni* or *ashmeadi* was not fatal to the *Lfa* workers, but caused crippling for 10-15 minutes. They were more aggressive until the toxin effect was reduced, and attempted biting the *Ca* workers. *Ca* workers also showed escape behavior after 3.3-4.9 hours of assault. After the population was reduced by the third attack of the *Lfa*, the *Ca* scouting guard apparently explored an escape route. It reentered the nest, antennated its nest-mates, and a mass escape followed. The egg mass and small larvae were transported either between the mandibles or on the spatulate stings, similar to *C. atkinsoni* workers. The queen escaped along with 3-7 guards during 5 attempts, 10.8-29.7% of the colony escaped. The unbudded colony was invaded and killed by the *Lfa* workers during subsequent attacks. In the captive conditions, the escaped workers and the queen were also killed. Under natural conditions, however, such budding colonies could establish new nests.

Both *C. atkinsoni* and *ashmeadi* were seen to escape in the groups of 10-15 workers. They aggregated at the escape sites and the peripheral ants stayed still, holding their heads parallel to the surface, spreading their legs more than usual, and making very slow undulating antennal movements. No attacks were exhibited by the nearby *Lfa* workers towards such *C* or *Ca* workers. However, prolonged immobility was not seen. The *C* or *Ca* workers broke the aggregates and were attacked by the *Lfa* over a period of 13-30 minutes.

Crematogaster minutissima Mayr

Habitat

C minutissima inhabits more humid situations such as stream sides and pond shores than the preceding species. It was found arboreally in the pithy twigs and stems of Hercules' club (*Aralia spinosa* L.), sumac (*Rhus* spp.), *Magnolia* spp., under the bark of *Quercus* spp., and in the reeds of *Smilax* spp. The colonies were small, containing about 200-1500 workers and several egg-laying queens (3-14). In the laboratory, this species nested in vertical glass tubing.

Colony defense

The workers of *C minutissima* (Cm) are about 3/4 the size of *C atkinsoni*. Colonies containing about 1000 workers were exposed to *Lfa* colonies. When the passage between the Cm colony and the *Lfa* colony was opened, an *Lfa* minor reached the Cm colony within a 15-30 minute period. The Cm workers at the nest opening opened their mandibles, slightly raised their comparatively bulbous gasters, and poured out in groups of 10-16. They followed the *Lfa* worker, bit its appendages and severed them. The next *Lfa* worker was similarly killed. After each assault, the Cm workers reentered their nest with a few (2-3) workers staying outside. A group of *Lfa* workers reached the Cm nest after 2 hours. Some (3-4) *Lfa* workers returned during this assault and the *Lfa* colony was agitated. Over 200 *Lfa* minors and media followed towards the Cm nest within the next 15 minutes. Only 10.4% of the *Lfa* workers exhibited gaster-flexing posture and mandibular attacks were predominant. The *Lfa* workers bit at the antennae, petiolar region, legs and cervical areas of the Cm workers which were 1/2-3/4 the size of the *Lfa*. The Cm

workers were lifted in the air and transported. Epinotal spines of the Cm workers are comparatively small and afford little protection to the petiole from *Lfa* mandibles. Also, the gaster of this species is larger than that of the preceding species of *Crematogaster*. Its toxin caused a temporary irritation in the *Lfa* workers. Repeated topical application of the gastric toxin disabled the antennae of transporting *Lfa* workers in one experiment, 44 *Lfa* were killed because of the poisonous effect of the toxin secreted at the base of the Cm sting.

The *Lfa* workers continuously invaded the Cm nest and attacked and stung their victims. The Cm nest is made up of pithy galleries. The *Lfa* workers nibbled the pith out for several minutes (30-120) before they reached the deep seated queens and the brood. If the attack was reduced, *i.e.*, if only 30% of the workers were killed, the Cm workers showed a mass escape (36.0-42.7% colony escape), no escape sites were scouted (Appendix 4). The escapees were easily attacked by the *Lfa* workers in captive colonies. The assaults were completed within 5-8 hours and the Cm colony was subdued by the *Lfa*. The *Lfa* majors did not take part in the assault.

The Cm nest structure provided some colony protection and the Cm toxin was fatal to the *Lfa* in large quantities. Small colony size and soft cuticle increased the vulnerability of the Cm colony. The Cm queens and their guards were defensive; they bit the attacking *Lfa* workers. However, gregarious assaults by 3-10 *Lfa* workers subdued all defensive attempts. The brood, queens and the Cm workers were used as food by the *Lfa*.

SUBFAMILY. PSEUDOMYRMECINAE

Tribe: Pseudomyrmecini

Pseudomyrmex pallidus F. Smith

Habitat

P. pallidus inhabits lakeshore vegetation, pines, hardwoods, and fence lines. This arboreal species was found nesting in the reeds of such pithy plants as *Cephalanthus occidentalis* L. and *Eupatorium* spp., that grow along the lakeshore. It also nested in wilted oak, magnolia, sumac and pine twigs, culms of bamboo and perennial grasses, and in profusely occurring climbers such as *Vitis* spp. and *Smilax* spp. Wherever it nested, *P. pallidus* was found to select upright, vertical, dried *Catalpa speciosa* twigs over its horizontal twigs (Appendix 5). The colony size varied from 47-113 individuals and had 1 to 3 laying queens.

The nests consisted of several cigar-shaped compartments so that only one ant could pass at a time through their connecting passages. At the top there was a pinhole-sized nest opening for a guarding ant. The brood was arranged with eggs in the upper compartment and larvae and pupae in the lower compartments. The queen and nurse ants, mostly callows, stayed in the nest and continuously moved the brood. This species was raised in upright or inclined glass tubes in the laboratory.

Colony defense

The passage between an *Lfa* colony and a glass tube or twig-nesting *P. pallidus* (*Pp*) colony was opened. For about 15 minutes *Lfa* minors made individual forays towards the *Pp* nest. As soon as one of them encountered a foraging *Pp* worker, it stopped. The *Pp* worker retreated and was followed

to its nest hole by the *Lfa*. This scouting *Lfa* laid a recruitment trail back to its nest by running forward, moving back a short distance, and repeating the sequence until it encountered another *Lfa* worker. It then reached its colony without stopping. The ants it encountered followed the recruitment trail and reached the *Pp* nest entrance. The nest entrance was wide enough for a single *Pp* worker to pass through. The sides of the opening were nibbled by the first *Lfa* reaching it until the guarding *Pp* reached and touched its antennae to the *Lfa* worker. The *Lfa* worker turned back but immediately returned to the nest entrance, opened its mandibles and made its way inside. The "alerted" *Pp* guard worker made several back and forth movements, vibrated its body as a "distress signal," opened its mandibles, moved forward, and immediately bit the mandibles of the intruding *Lfa*. Within a fraction of a second, the *Lfa* was pushed out and lifted into the air when the nest entrance was reached. The lifted *Lfa* secreted a venom droplet at its sting, curled its abdomen, and either applied the drop topically or subcutaneously to the head of the *Pp* before the *Lfa* was thrown out (Fig. 6).

If the intruder was held for over 30 seconds both the ants fell outside the nest entrance. It took 4.25 minutes (mean of 10 nests) for the *Lfa* to encounter and become chemotactically and/or visually "alert," and to invade the *Pp* nest (Table 9). When workers of both species were confined in a petri dish, the chemotactically alert ants followed each other and resumed attack response within 3-31 minutes (Table 10).

The guard ant was replaced by the ant behind. There was a short time lapse from this replacement to the next nest invasion by an *Lfa*. In the course of time, the *Pp* alate males, females, and the workers were seen to escape the nest by flying or swiftly running through

Figure 8. Expulsion behavior in arboricolous species.

1. *Camponotus* (*Colobopsis*) *impressus* (C) expelling a nest-invading *S. invicta* worker.

2. *Pseudomyrmex pallidus* (Pp) expelling a nest-invading *S. invicta* worker.

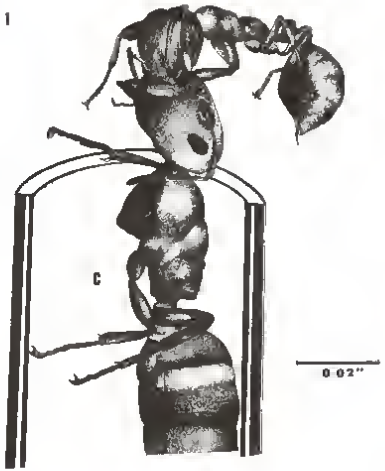

1
C
0·02"
2
P_1

Table 9 Time interval (in sec) between contact chemoreception and nest invasion between *Solenopsis invicta*, *Pseudomyrmex pallidus* and *P. brunneus*.

	P. pallidus	*P. brunneus*	Student-t
Range	105-733	625-1125	
Mean	301.00	751.00	Significant ($P = 0.05$)
S.D.	242.30	147.16	

The scouting *S. invicta* worker antennated a foraging *P. pallidus* or *P. brunneus* worker outside the tube nest and then entered the nest ($n = 11$).

Table 10. Time lapse (in min) between "alert" to "attack" responses of the red imported fire ant in *Pseudomyrmex pallidus* and *Pseudomyrmex brunneus* (n = 10).

	P. pallidus	*P. brunneus*	Student-t
Range	3-31	3-22	
Mean	10	9	N.S.
S.D.	9.21	6.43	

the nest entrance. In 5 experiments, the percentage of workers escaping varied from 2.94-29.79 (Appendix 4). After about an hour's struggle between the guards and invading *Lf.* workers, the attacked guard ants retreated into the nest, smeared venom onto callow nurse ants, and agitated the whole colony. Some nurse ants entered the lower compartments and moved the eggs, pupae, and larvae around the laying queen in the lowermost part of the nest.

Removal of the brood to the lowest nest part was considered protective provisioning since the alien ant reached this part only after opening the narrow passage of at least 3 compartments (in natural twig nests). The nurse ants were attacked, stung, and transported by the *Lf.* workers. The invading *Lf.* were seen to show a continuous gaster-flexing movement for 3-25 minutes inside the *Fp* nest. It was followed by entrance into the nest by several *Lf.* media and minors and removal of the brood. The queen showed some aggressive behavior by opening her mandibles and attacking the *Lf.* workers. However, the queen was stung and her gaster was severed by a media worker. The *Lf.* workers overcame natural twig nests within 8.5 hours, while they overcame the glass tube nests within 5.5 hours (mean of 5 experiments).

On confining equal numbers of *Lf.* and *Fp* workers in petri dishes, a specific response pattern was followed by the *Fp* workers during confrontation. These responses were analyzed. The frequencies of two or more cumulative responses occurring within the first 20 minutes are shown in Table 11.

The *P. pallidus* venom was fatal to the *Lf.* workers when they repeatedly were stung on the head. Such *Lf.* workers curled their abdomens, bent their heads, straightened their appendages, and died within 10-15

Table 11. Frequency of two or more cumulative responses occurring within first 20 min of confrontation between *Pseudomyrmex pallidus* and *Solenopsis invicta* (mean of 3 replications).

Responses	Frequency	% of total responses	Mean frequency
A + B	36	7.98	12.00
A + B + C	49	11.08	16.67
A + B + D	56	12.12	18.67
A + B + E	27	5.98	9.00
A + B + F	22	4.88	7.34
A + B + G	22	4.88	7.34
A + B + H	21	4.66	7.00
A + B + I	77	17.73	15.67
A + B + J	34	7.54	11.34
E + K	108	23.95	36.00
L	8	1.77	2.67
Total responses	451		
Mean responses	13.67		

A through D are "alarm" responses, and E through K are "attack" responses. For response codes see text.

minutes. However, such mortality was confined to assaults between the guard workers and the invading *Lfa* workers.

Pseudomyrmex brunneus F. Smith

Habitat:

P. brunneus inhabits lakeshore, pine, and hardwood vegetation, nesting in the dry pithy twigs of *Cephalanthus occidentalis* L., *Eupatorium* spp., sumac, *Morus* spp., and oaks, in culms of bamboo and perennial grasses, magnolia twigs, pine branches, and dried stems of climbers in the mesophyllic hammocks. The ants colonized twigs bored by pyralid and cerambycid larvae. The colonies consisted of 30-200 individuals and 2 to 3 fertile queens in the larger colonies. The nests were very much like the *P. pallidus* nests and most of the twigs occupied were vertical. This species was found with *P. pallidus*, *Crematogaster* spp., and *Camponotus* (*Colobopsis*) *impressus* on *Cephalanthus occidentalis* L.

Colony defense:

Both the natural nests and artificial glass tube nests were used to expose the *P. brunneus* (*Pb*) colonies to the *S. invicta* (*Lfa*) colony. When the passage between the colonies was opened, an *Lfa* minor laid a recruitment trail similar to that in the *P. pallidus* experiment. As soon as the *Lfa* encountered a foraging *Pb* worker on the latter's nest, the *Pb* retreated but was followed by the *Lfa* worker. Eventually, following the chemotactic response, the *Lfa* reached the *Pb* nest 10 h-18.75 minutes after encountering the first *Pb* worker outside the nest. The guarding *Pb* thrust its head out and antennated the *Lfa*, retreated slightly, flexed its abdomen (distress signalling), and stayed with its mandibles open in the nest entrance. The *Lfa* minor entered the nest, came out,

repeated the sequence 2-5 times, and then encountered the guarding *Pb*. The *Lfa* opened its mandibles and grasped those of the *Pb*. Within a fraction of a second, the *Lfa* was pushed back by the *Pb*, lifted in the air at the nest entrance and thrown out (expulsion behavior). Here also, the guarding ants were replaced by ones immediately behind them, and were eventually venomed by the *Lfa*. From the time the *Lfa* became visually and chemotactically "alert" to the *Pb* presence until it stung the *Pb* worker, there was a lapse of 3-22 minutes. There was no significant difference in the time lapse between the alert and attack response of the *Lfa* for the two species of *Pseudomyrmex* (Table 9). During the time between the two invasions of *Lfa*, alates of *Pb* were seen to fly from the nest entrance. Some workers also escaped the nest. The percentage of colony escape was 2.25-23.21 in 5 colonies (Appendix 4). The escaped ants were not allowed to reenter the nest by the guard ants. The guard ants were replaced 3-7 times, after which the *Lfa* encountered no resistance. The *Lfa* stung by the guarding *Pb* extended their appendages and died within 10-15 minutes. The tenerol nurse ants removed the brood to the lowermost compartment and the queen was protected by arranging the larvae and pupae around her. The callows and the *Pb* workers were stung by the *Lfa* and they died within 4-13 minutes. The invading *Lfa* minors and media flexed their abdomens for 5-10 minutes and then began transporting the dead *Pb* callows, brood, and the gasters of severed queens to their own colony.

The *Lfa* workers overcame the *Pb* colonies in glass tubes within 6.25 hours, and the natural nests within 11 hours. The pattern of defensive responses (alarm and attack) was the same as for *P. pallidus* when the *P. brunneus* workers were confined with the *Lfa* workers in petri

dishes. However, the frequency of some events differed between *pallidus* and *brunneus*. More aggressive responses were shown by *P. pallidus* than by *P. brunneus*, although the number of workers used was the same (100 *i.f.* to 100 *Pp* or *Pb*). However, alarm responses were approximately the same in both species. The proportion of attack responses was significantly higher in *P. brunneus* than in *P. pallidus*. For detailed analysis of responses, see Tables 12 and 13.

Aggressive responses by *P. brunneus* and *P. pallidus*

P. brunneus individuals showed less total alarm (alert and activation) and attack responses (seizing, pulling, and stinging) than *P. pallidus* towards the *S. invicta* workers (Table 11). Seizing, dragging and stinging responses were twice as frequent in *pallidus* as in *brunneus*. However, the pattern of aggressive responses, *i.e.* alarm and attack responses, was similar in both species. The *S. invicta* workers showed gaster-flexing, oozing of venom droplets at their stings, and antennation of nest-mates that apparently "attracted" many *i.f.* workers to the site of the assaults. It was seen that more *P. pallidus* and *P. brunneus* workers were killed by topical smearing of *i.f.* venom than by stinging

Table 12. Frequency of two or more cumulative responses occurring within first 20 min of confrontation between *Pseudomyrmex brunneus* and *Solenopsis invicta* (mean of 3 replications)

Responses	Response frequency		
	Total	% of total	Mean
A + B	15	7.35	5.00
A + B + C	16	7.84	16.00
A + B + D	26	12.74	8.66
A + B + E	21	10.29	7.00
A + B + F	5	2.45	1.66
A + B + G	9	4.41	3.00
A + B + H	8	4.40	2.67
A + B + I	30	14.70	10.00
A + B + J	6	2.94	2.00
E + K	45	22.05	15.00
L	22	10.78	7.33
Total responses	204		
Mean responses	6.18		

Alarm responses P *pallidus* and *brunneus* not significant ($P = 0.01$)

Attack responses sigaificant ($P = 0.01$).

Table 13. Frequency of aggressive responses shown by *Pseudomyrmex pallidus* and *P. brunneus* to *Solenopsis invicta* within first 20 min of confrontation

Species	Alarm	Attack	Total	% of total Alarm	% of total Attack
P. pallidus	141	240	443	31.83	54.17
P. brunneus	57	125	181	31.49	69.06

SUBFAMILY: DOLICHODERINAE

Tribe Tapinomini

Iridomyrmex pruinosus (Roger)

Habitat:

Iridomyrmex pruinosus was found nesting in open, cultivated, fallow fields and ecotones between pine and mesophyllic ecosystems. The mounds made by *I. pruinosus* range from 7-15 cm in diameter, circumscribing 1-6 separate nest openings interconnected only by above-ground trails of ants, through a distance of 30 cm to 5 meters. These ants were active during warm sunny days when the temperature ranged from 25-35°C and even on overcast days at 26°C. The trailing ants followed the preceding ant, keeping a distance of 1-2 mm. The colony size varied from 1000-4000 workers, one queen was found in each colony. This species apparently is in taxonomic flux, the sordid brown form occurring in Florida was studied.

Colony defense.

Colonies of *I. pruinosus* (*Ip*) and *Lfa* both consisting of 1500 workers were connected. The *Lfa* workers were the first to invade the *Ip* nest area. The confrontation began after 15 minutes. The foraging *Ip* workers came near the invading *Lfa* minors, touched their antennae to the head and abdominal portions of the *Lfa*, circled around them, touched their antennae to those of the *Lfa* workers and moved away. The foraging *Ip* apparently transmitted an alarm message to its nest-mates by touching their antennal tips. The *Ip* workers were seen to enter their nest and apparently agitate the whole colony. Several *Ip* workers emerged. The *Ip* workers stayed parallel to the *Lfa* workers at a distance of 3-4 mm, directed their antennae towards the *Lfa*, slightly raised their abdomens, and sprayed a

secretion two or three times before they moved away. The *Af* worker flexed its abdomen and after 2 seconds, groomed its antennae by passing its scapes through the labial part. It lowered its abdomen, almost touching the ground.

The second attack by the *Ip* workers involved touching antennae to the *Af* tibiae. The *Ip* workers retreated, raised their abdomens and sprayed towards the spot the antennae touched. The *Af* opened its mandibles, closed them, and walked with alternate raising and lowering of its abdomen. The *Af* that received sprays from more than 10 ants or was sprayed more than 10 times, held its antennae straight up, passed its antennae through its mandibles biting them slowly and abnormally, and showed crippled locomotion and paralysis. It was not attacked again for 7.5-16 seconds. However, it was attacked when it showed leg movement, however slight. The third attack response involved mandibular biting of the *Af* appendages and antennae. The moving *Af* fell several times and was extremely aggressive to the *Ip* workers around it. It bit them and killed at least one *Ip* before it died after 1 hour.

The *Ip* workers that attacked the hind legs of *Af* eventually were brushed with venom (32 cases). The brushed ant groomed its antennae for 45 seconds to 3 minutes. The *Ip* worker was crippled after 4 5 minutes and died after 7-10 minutes. *Af* workers did not sting the *Ip* workers. The *Ip* workers sensed the *Af* workers without contact and in many cases (127) sprayed them immediately, an apparent physio- or chemotactic response. When one third of the above-ground *Ip* workers were killed, the repletes inside the brood cells removed the brood to the lowermost nest cells. The *Ip* nest tunnels are straight with 1-3 cm cells extending from them. An escape response followed after 2 hours when the nurse ants and repletes carried the brood, and when the queen (yellow thorax) came

out of the nest hole. The *Lfa* workers followed these workers and opened their mandibles. Biting was not observed until the *Lfa* touched their sting to the *Ip* cuticle and venomed them. The venomed *Ip* workers showed digging behavior for 3-5-4 seconds and then died within 7 minutes. The queen showed no defense except for its increased rate of locomotion. It was attacked at its petiole and cut into two parts.

The *Lfa* workers entered the *Ip* cells and removed the rest of the *Ip* brood. They killed any workers they found and carried them out. The workers were piled near the nest and the *Ip* larvae were used as food. The *Ip* colony was overcome within 6-24 hours by the *Lfa*. For some unknown reason, the *Lfa* majors did not enter the confrontation.

Confrontation index

Though the *Ip* workers showed colony defense and emitted repulsive, slow action chemicals, a large number of *Ip* workers died due to topical poisoning by *Lfa* venom. The 24 hr confrontation index was 19.64, *i.e.*, about 20 *Ip* workers were killed for each *Lfa* worker killed.

Conomyrma flavopecta (M. Smith)

Two species of *Conomyrma*, one orangish yellow, possibly *flavopecta* (M. Smith), and the other sordid brown to black, *insana* (Buckley), are found in North Florida. They both are monomorphic and monogynous species.

Habitat

The yellow species, *C. flavopecta*, inhabits open or partly shaded areas in fallow, cultivated, or mowed fields. It made singular, 7-12 cm crater-shaped mounds, 5-6 cm high, and with centrally located exit holes. Occasionally, 2-5 interconnected mounds extended adjacent to each other

at different elevations. On the average, the colony size varied from 500-800 individuals. The mounds of this species were seen right beside the *S. invicta* mounds or within 15 cm to 2 meters from it. The *C. flavipecta* tended to be scavengers, often feeding on dead fire ants.

Colony defense

The colonies consisting of about 700 ants were connected to the *Lfa* colonies (1500 ants). The *C. flavipecta* (Cf) workers were seen to forage around the *Lfa* nest area and make fast darting movements. The foraging *Lfa* minors reached the Cf nest after 10 minutes and were frequently antennated by the Cf workers. The Cf that encountered the *Lfa* congregated and groomed, exchanged food, followed by social grooming. They antennated the nest-mates joining the group and dispersed after 2-2-3 minutes. The Cf workers momentarily antennated the *Lfa* and opened their mandibles. The *Lfa* workers responded by assuming a gaster-flexing posture. The gaster-flexing *Lfa* waved their antennae to the side of the clustering Cf workers and moved sideways and backwards waving their stings (gasters) until they brushed on some of the Cf workers. The clustering Cf workers dispersed immediately, a number of them had been smeared with the *Lfa* venom. The venomed workers retreated, turned their heads down, and moved near the gasters of the *Lfa* and were topically impregnated with venom (attraction). They walked faster than normal, at random and lacking coordination, rubbed their legs on the substratum, bit their own dead, and died within 3.25-5 minutes.

The *Lfa* exhibited mandibular attacks after 20 minutes and stung all the Cf workers encountered. The attempts took 2 seconds. On the other hand, the Cf workers also followed the *Lfa* minors, attacked them at the petioles, lifted and carried them. In one experiment, 19 out of 80 cases

showed *Cf* attacks on the *Lfa* legs, 6 on the antennae, 3 on the petiole, and the rest showed darting movements around the *Lfa* workers. All the *Cf* attacking the *Lfa* showed *Lfa* toxin effect and subsequently died. The dead and dying *Cf* workers were bit on their abdomens by the *Lfa*, apparently to obtain food. The heads of the *Cf* were cut off and were left behind. In some specimens even the legs and antennae were cut off. The *Lfa* venom was attractive to the *Cf* workers since they were seen to lick it.

The *Cf* workers were not immediately attacked by the *Lfa* and apparently the *Cf* had a repulsive defense mechanism. However, the *Cf* workers held onto the *Lfa* appendages and retarded their locomotion in some cases. Such *Lfa* workers were seen dead after 24 hours. The *Lfa* workers (only miners) entered the *Cf* colony only after the majority of its workers were killed (3-4 hrs) and entered the comparatively straight tunnels (Fig. 9, *Cf*). The brood cells were emptied and the queen was killed. Its abdomen was sucked by 6 workers. The brood transport was done in installments showing the repellant activity of the nest tunnels that were off after 10-18 hours. The tunnels were not destroyed. The dead *Cf* were piled up by the *Lfa*.

Confrontation Index

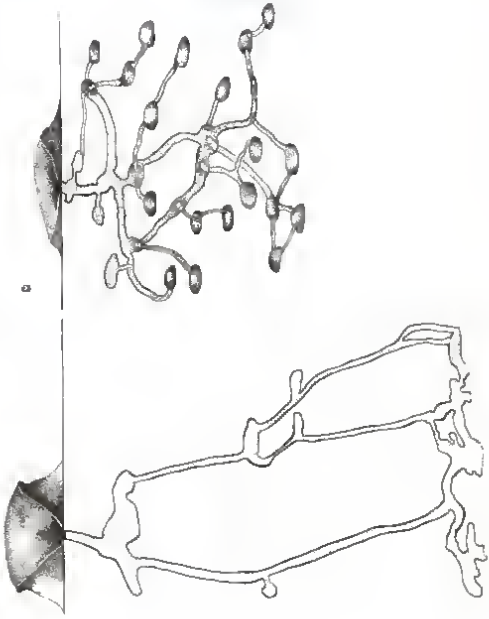
The index was 9.85 during the 24 hr confrontation between the *Cf* and *Lfa* workers, *i.e.*, about 10 *Cf* workers were killed for each *Lfa* worker.

Conomyrma insana (Buckley)

Habitat

The sordid brown to black species, *C. insana*, often nested in bare and hard soil along dirt roads, open sunny areas in cultivated and fallow fields, and along fire lanes. It made 3-5 cm slanted mounds with eccentric exit holes. From 6-17 mounds of the dark form were usually

Figure 9. Nest structures of *Coptotermes* (*Leptocoptotermes*) (Cf, depth 36 cm) and *Coptotermes crassus* (Cc, depth 22 cm).



connected by a surface trail to form a single colony. The colonies ranged from 1000-6000 individuals. The dark form was predacious on arthropods and was not seen to nest close to *S. invicta* or *S. geminata* colonies. It was found to prey on fire ant queens after nuptial flights.

Colony defense

A colony of 1500 workers of the black form of *C. ruginoda* (Cr) was exposed to a colony of 1500 *Lfa*. The *Lfa* miners were the first to enter the Cr nest area; this took place during the first 15 minutes. The Cr workers antennated the *Lfa* worker. The *Lfa* worker retreated and exhibited gaster-flexing posture, oozing the venom drop at its sting. The Cr workers showed frequent antennation of the *Lfa*, grooming and clustering after 4-5 minutes. The *Lfa* workers also moved near their nest-mates and groomed their antennae. The Cr workers darted over them, opened their mandibles, and attacked their appendages. The *Lfa* workers dispersed and attained gaster-flexing posture. A remarkable attraction was shown by the Cr workers toward the *Lfa* venom. They licked it as they did aphids they tended, and antennated the *Lfa* gaster while doing so. The ants licked the *Lfa* venom until their antennae curled and they jerked back. They rubbed their head in the soil and apparently recovered after 5 minutes, but their antennae were still curled and functionless. Such Cr workers stayed around the *Lfa* and died within 15-28 minutes.

The Cr workers entered their nests and groomed. The colony showed escape response after 3 hours when the workers were seen to hold their immatures between their mandibles and come out. The *Lfa* were aggressive towards them and attacked at their heads, legs, and gasters. Within 20 minutes of attack, most of the Cr ants died due to *Lfa* venom (80/100), 5 showed cervical attacks and the rest abdominal attacks.

I♀♀ workers attacked any escaping C♂ workers and piled its dead, but they did not enter the C♂ nest because of the narrow and proliferated nest cells (Fig. 9, C♂). The queen escaped attack together with 3.2% of the colony (average of 5 colonies) for 24 hours. She was attacked as soon as she left the nest. Wide dispersal of nest exits also added to the protection of the brood and queen cells.

Confrontation index

Comparatively more workers were killed in the case of C♂ than C♀. The confrontation index was higher (26.05). Only the 4♀♀ workers that were attacked at their appendages and antennae by the C♂ died. On the other hand, the C♂ workers defended their colonies better because of the repellent chemical mechanism and because of the nest structure.

SUBFAMILY FORMICINAE

Tribe: Formicini

Lasius neoniger Emery

Habitat:

This species is abundant in the northern part of the United States and its range extends to North Florida. At Tall Timbers the species nested in open areas and under trees shade that would receive the noon-time sun part of the day. On the average, 1.2 mounds were seen per square meter of area. *L. neoniger* builds loose dirt mounds about 7015 cm high and they are interconnected with other mounds as distant as 15-50 cm through a partly excavated 1 cm wide tunnel covered with a loose soil shade. In open mesophyllic hammocks, the ants also occupied termite-infested hardwood logs. The colony size varied from 370-500 individuals.

Colony defense:

Colonies of *L. neoniger* (*Ln*) containing about 400 ants were exposed to the *Lfa*. The workers of both species entered the confrontation area. Since the *Ln* workers moved faster, they confronted the *Lfa* minors that were just moving out. As the workers confronted, they touched their antennae for a second or two and then the *Ln* workers retreated, and touched their antennae to those of the nest-mates, their femur and tibiae were also touched. Similar "message transmission" was seen in the *Lfa*: the workers touched their antennae to those of the nest-mates. The *Lfa* colony was agitated within a minute's time. A file of *Lfa* workers, majors, minors and media, entered the confrontation area, and as soon as encountered by an *Ln* worker they attained gaster-flexing posture.

droplets of venom appeared on their vibrating stings within 0.3-0.5 seconds. The *Ln* workers quickly grasped the flagellar portion of the *Lfa* antennae between their mandibles and clypeus, pulling them through while allowing slack (Fig. 10). The antennal cuticle apparently did not lose many of its sensors but was affected by the mandibular secretion. The *Lfa* workers did not move away or change their posture, and waved their free antennae. The *Ln* worker moved away, curled its abdomen beneath its thorax, and squirted poison, directing it towards the frontal area, antennal sockets, clypeus, and mouthparts of the *Lfa*. The *Ln* worker again touched the *Lfa* antennae and moved away. The *Lfa* worker spread its legs wider, dropped its gaster, and moved with some antennal motion. It was again squirted with toxin by the surrounding *Ln* workers and died within 20 minutes. The *Ln* workers held their gasters laterally or even straight backwards to squirt the acidopore secretion during the assaults. The spray was seen to reach a distance of 4-5 mm.

The fast moving (darting) *Ln* workers contacted the *Lfa* venom from the workers flexing their gasters, and showed the effect. They moved faster, repeatedly groomed their antennae with their fore epiphyses and their gasters with their hind legs. The action ceased after 3-4 minutes. However, when the *Ln* worker contacted the *Lfa* venom 3-4 times, it curled up and fell down dead within 7 minutes. After 10 minutes, several dead ants were seen in the 4-5 cm confrontation area and the *Ln* workers walked over them. The *Lfa* workers slowly shoved the dead ants in front of them and reached the *Ln* nest area. Twenty-four hours later, most of the confrontation area was occupied by the *Lfa* workers. The *Ln* workers moved all the immatures and the queen deep into the nest and collected pieces of wood around the entrance of their nest. The barrier was easily

Figure 10. A *Lasius neoniger* worker grasping the flagellar portion of *S. invicta* antenna between its mandibles and clypeus, pulling it through while allowing slack. (Magnification 200X).

removed by the *Lfa* workers and they made their way into the *Ln* nest. The *Ln* workers on the nest surface attacked but were killed by the *Lfa* workers. The *Lfa* workers also exhibited more mandibular than stinging attacks and removed many guarding *Ln* workers from the entrance tunnel. The *Ln* nest tunnels were wide enough for the *Lfa* to make a passage. Each guard was attacked, killed, and piled outside the nest. The "nurse ants" did not show aggression and the queen was seen only to open her mandibles. The alates showed no resistance and were immediately attacked. The queen was beheaded and her gaster was removed. Pupae were removed from the cocoons and transported. The colony of *Ln* was subdued within 24-36 hours.

Ln secretions from the acidopore were toxic to the *Lfa* and so were the *Ln* mandibular secretions. Also, the *Ln* workers tolerated the *Lfa* venom during the first topical application and apparently recovered, but the *Lfa* workers died of the *Ln* toxins.

Confrontation Index

The 24 hr confrontation index was less than one (0.45), *i.e.*, two *Lfa* were killed for each *Ln* worker, since mortality of *Lfa* was 313 and that of *Ln* was 133. At localized areas on Tell Timbare where *Ln* population was abundant (Beadle Course, Hall and Sheep Islands) the *Lfa* nests were reduced or absent.

Paratrechina (Nylanderia) sp.

Habitat

The genus *Paratrechina* has been noted for its complexity (Creighton 1950), and many Floridian species are undescribed. One species of the subgenus *Nylanderia* is treated here since it was common to mesophyllic

hammocks and pine barrens. This species nested hypogaeically and made 3 cm craters above the ground. Immediately after rains, it was found nesting epigaeic, in the leaf litter, under the rotting bark and moss. Its colony size varied from 30-160 workers; there was a single queen.

Colony defense

Large colonies of *Paratrechina* (*Nylanderia*) sp. (P) containing about 150 workers, were connected to the *Lfa* colonies (about 1500 workers). P workers were fast both in movement and in sensing the alien odor. Six darting workers entered the confrontation tube. One of them stopped at about 4 cm distance, waved its antennae faster than usual, and went near the entrance of the *Lfa* colony. Before encountering any *Lfa* worker, it turned back, struck its antennal flagella against those of its nest-mates, holding the flagella parallel, outward and elevated. Each of the encountered nest-mates darted towards the *Lfa* colony, showing that the antennal communication was stimulating the alarm behavior. The alarm response was also due to physiochemical stimuli from the *Lfa* colony. To show this, loosely packed cotton wool was placed in the confrontation tube of one of the colonies. P workers were the first to reach the cotton fibers and make their way through until they reached near the *Lfa* colony. The whole reaction was completed within 5 seconds to 1 minute. The *Lfa* workers also emerged from their colony and made their way up to the P nest. As soon as workers of both species approached within 0.5 cm of each other, the *Lfa* workers exhibited gaster-raising posture, bent their heads near the ground, and secreted a droplet of venom at their stings. The P worker bent its gaster beneath its raised legs, opened its mandibles, and directed a toxin spray from its acidopore towards the head, alitrunk, and abdomen of the *Lfa*. The *Lfa* workers showed differential toxicity to the

P toxin, depending on the morph of the worker; the majors (6 mm) showed the effect within 3 seconds while the minors showed it after 1 minute. The effect was attributed to the greater amount of cuticle exposed to the toxin by the majors. The sprayed *L.fla* workers were surrounded by 2-3 P workers and attacked again. A single P worker was seen to hold the squirting posture for 3-5 seconds. The *L.fla* showed crippled locomotion, abnormal stretching of the antennae, loss of stinging posture, extreme aggressiveness (shown by biting even their nest-mates), and death after 10-15 minutes. The dead and dying *L.fla* workers were repellent to the *L.fla* and P workers.

The P workers were not bitten or stung by the *L.fla* workers. During their fast darting movements, the P workers contacted *L.fla* venom. The topical poisoning momentarily intensified their darting movements, followed by curling of their abdomens, and death within 5-7 minutes. A further maneuver of attack was shown by the *L.fla* workers when they invaded the P nest and surrounded the queen. They raised their stings and slowly moved backwards, their antennae making a slow movement in the direction of the queen. The movement stopped when the venom was applied to the queen's cuticle. The venomed queen was grabbed by 4-6 minors and bitten at her petiolar region. She made mandibular attacks on the *L.fla* workers, but her gaster was severed by the *L.fla* workers. The callows and the nurse P workers were passive and were easily killed. The whole colony attack was complete after 4-5 hours. Smallness of the P colony was a definite weakness during this assault, apart from the simple nest structure.

Confrontation index

Groups of 100 workers of *L.fla* and P were used. During 4 experiments, the 124 P workers and 305 of the *L.fla* workers were killed over a period of

24 hours. The C. I. was 0.406, i. e., about 2 *Lfg* workers were killed against one of the *Paratrechina* sp.

Formica schaufussi dolosa Wheeler

Habitat:

F. schaufussi dolosa inhabits open pastures, mowed fields, and pine woods. This species was not abundant on the Tall Timbers' property and was found in the areas where *S. invicta* populations were sparse. The colonies of *F. s. dolosa* were represented by a single 1 cm nest opening and no apparent mound. The colony population was nearly 2000 individuals; a polygynous condition was suspected due to the occurrence of many queens (7-30).

Colony defense:

The colonies of *F. s. dolosa* were raised in rectangular plastic nests and Wilson cells. When the colonies were connected to the *Lfg* nests, the *F. s. dolosa* (Fs) workers first made their way to the confrontation tube. One Fs worker entered the *Lfg* nest area, stopped 3 cm from the nest opening, slowly waved its antennae, and opened its mandibles. It then darted back and touched the antennae (tips of flagella) and vertex of a nest-mate. This response (message) was transmitted among other Fs nest-mates and the whole Fs colony within 13 minutes. The "messenger ant," together with 4 others, reentered the *Lfg* nesting area and encountered an *Lfg* minor on its way. Three or four swift antennal contacts between the Fs and *Lfg* workers elicited defensive response. The Fs worker raised its legs upward, brought its antennae parallel, moving them to the direction of the *Lfg*, secreted a liquid between its mandibles (mandibular alarm-defense secretion), curled its gaster under its alitrunk and with a

jerking motion, squirted the contents of its Dufour's gland via the acidopore towards the *Lfa*. The poison was received cephalad by the gaster-flexing *Lfa* worker which in turn secreted a venom droplet at its sting. The *Lfa* workers emerging from the nest touched their antennae to those of the gaster-flexing *Lfa* and returned. The *Lfa* colony was agitated within the next 7 minutes, and a fast moving file of over 30 majors, miners, and media started towards the site of confrontation. The *Lfa* workers coming near (1-3 cm) the *Fs* workers exhibited gaster-flexing and stopped. The *Lfa* venom elicited alarm and defense frenzy in the surrounding *Lfa* workers. A second attack response was shown by *Fs* workers; the *Lfa* worker sprayed with toxin was grasped at the antennal flagella and released, causing injury to flagellar segments 3-6. The attacked *Lfa* worker moved in a circular motion, rubbed its foretarsi along the antennae, and fell on the side. One or more *Fs* workers attacked the *Lfa* appendages as the third response followed. *Lfa* workers responded to the appendicular attacks by mandibular grasps and stinging. Pulling and dragging response was also shown by a nearby *Fs* worker; it dragged the attacking *Lfa* away from the *Fs* being attacked. Some *Fs* workers attacked the gasters of the *Lfa* workers with their sharp, sulcate mandibles so that the hemolymph oozed out and they died within 6-7 minutes. Apparently, mandibular toxin hastened the fatality since mechanical tearing of the *Lfa* gaster with a pin caused the worker to die only after 20-25 minutes.

The *Lfa* workers were repeatedly squirted by the same *Fs* worker for 4-6 seconds and the action was continued by another *Fs* worker until the *Lfa* curled its body and showed no antennal movement. Four to six sprays were fatal to the *Lfa* workers irrespective of their size. Intensity of

mandibular bites was greater among the *Fá* workers than the *Lfα* workers. Venom application by the *Lfα* with minimal contact with the assaulting *Fá* worker reduced the opportunity for effective aggression on the part of the latter. Gaster-flexing, together with the apparent attractive effect of *Lfα* venom, elicited mandibular and cephalic contact of *Fá* workers to the *Lfα* venom. The venomed *Fá* workers died within 22-30 minutes. During 10 minutes following application of the *Lfα* venom, the *Fá* worker was more aggressive, it followed the *Lfα* workers and sprayed them repeatedly, the *Lfα* proceeded towards the *Fá* nest. More *Lfα* workers were recruited and a mass assault followed. The first *Fá* assault was fiercer than following ones. The *Fá* workers were bitten at their appendages, antennae, and petiolar regions by the more aggressive and more numerous *Lfα* workers. The mandibular bites attached the *Lfα* workers to the portions of the *Fá* bitten. The action reduced locomotion in the *Fá* workers and slowed the squirting responses. The *Lfα* workers raised their antennae upwards while attacking, protecting them from the bites of the *Fá* workers. Within 5 minutes, over 300 *Fá* workers emerged from the colony, but only 0.1% showed squirting and the rest showed biting response. Within 40 minutes of assault, 15% of the *Fá* workers crawled on the nest wall (escape response) and showed no aggression. Aggressive responses in both species are analyzed in Tables 14 and 15. The *Lfα* workers excavated the *Fá* nesting site and entered their wide tunnels (4 mm - 12 mm). A file that was 3 ants wide moved into the nest and killed the *Fá* workers for 5.2 hours. The *Fá* workers used mandibular attacks to defend the nest; even the callows were aggressive. The colony of *Fá* defended itself for 17-25 hours. Eventually, all the nesting area was occupied by the invading *Lfα* workers. The dead *Fá*

Table 14. Frequency of attack responses shown by *Formica schaufussi dolosa* towards *Solenopsis invicta* during 20 min of confrontation.

Responses	Parts attacked				
	Antennae	Mandibles	Thorax	Petiole & gaster	Legs
Saizing & severing	23.0	7.0	2.3	18.4	36.3
Spraying:					
-after seizing	0	2.4	0	1.0	35.0
-without seizing	0	23.0	3.0	15.2	17.1
Total	184.7				

Table 15. Frequency of attack responses shown by *Solenopsis invicta* towards *Formica schaufussi dolosa* during 20 min of confrontation.

Responses	Parts attacked			
	Antennae	Mandibles	Legs	Alitrunk & gaster
Seizing	3.6	16.4	8.3	0
Severing	3.0	0	10.5	60.8
Stinging				
-along with mandibular grasp	0	0	0	16.0
-without mandibular grasp, topically		0	0	11.0
Total	129.6			

workers were severed by the *L.f.a* majors and media and their abdomens were piled outside the nest. The pupae and larvae of Fa were stung and were taken to the *L.f.a* nest by the *L.f.a* workers. The queens of Fa were aggressive. They attacked the *L.f.a* workers at their mandibles and cervix and severed them. Over 13 *L.f.a* were killed by 2 Fa queens. However, they were eventually (after 32 min) bitten by 7-10 *L.f.a* media and 2-3 majors at the legs, gaster, and antennae and severed into pieces. The dead queens were not used as food but were piled with the workers. The Fa nest was deserted by the *L.f.a* 2 hours following the assault.

Confrontation Index:

Numerical analysis of the Fa workers against the *L.f.a* workers killed showed a C.I. of 2.086, *i.e.*, more than 2 Fa workers were killed for each *L.f.a*. In one experiment, 372 *L.f.a* workers were killed as opposed to 72 of the Fa.

Tribe: Camponotini

Camponotus (*Colobopsis*) *impressus* (Roger)

Habitat:

C. impressus is a dimorphic, arboreal species found nesting in the pithy twigs of Hercules' club (*Aralia spinosa* L.), sumac (*Rhus glabra* L.), button bush (*Cephalanthus occidentalis* L.), *Magnolia* spp., *Rosa* spp., *Vitis* spp., *Smilax* spp., and culms of bamboo and perennial grasses. The colony size of *C. impressus* varied from 30-360 workers. Usually a single fertile queen was found in a colony. This species inhabits lakeshore vegetation along with *Crematogaster atkinsoni*, *C. ashmeadi*, *Pseudomyrmex pallidus*, and *P. brunneus*.

Colony defense

Colonies containing over 300 workers were exposed to the *Lfa* colonies (about 1500 workers). First, a minor *Lfa* worker laid a recruitment trail from the glass tube nest of *C. amplexans* (*Ca*) to its nest. The trail was followed by 3 nest-mates after antennation. One of the *Lfa* minor workers confronted a foraging *Ca* minor. The *Ca* worker touched its antennal apices to the vertex and the antennal flagella of the *Lfa* worker and immediately moved away. The *Lfa* antennated its nearby nest-mates and reentered the *Lfa* colony which was partly agitated during the next 20 minutes. One of the nest-mates crawled over the *Ca* nest. The *Ca* forager reached its nest entrance, occluded by the cork-shaped cephalomandibular area of the *Ca* major worker (phragmatic behavior of the guard ant). The frontal cephalic area of a *Ca* major worker is punctiferous, with a single setose sensor emerging from the center of each of the punctures. Close observation of the cephalic sensors showed a group of 8 barbicles at their tips. Such sensors were equally distributed on the mandibles but were devoid of the barbicles (Fig. 11). The *Ca* minor feebly touched the flat head of the guard and was given a space to enter the nest. The *Ca* minor then antennated the workers in the upper compartment of the *Ca* nest. The *Lfa* minor reached the *Ca* nest entrance within 2.3-4 minutes after a series of up and downward movements. It antennated the nest enclosure, which was followed by a series (5-8) of retreats, antennation with its nest-mates, and ultimately mandibular biting of the guard's head. No movement was shown by the guarding *Ca* major. However, it opened its mandibles after a series of bites and slightly raised its head to clutch mandibles with those of the *Lfa*, lift the *Lfa* in air, and expel it (Fig. 8). An *Lfa* minor nearby showed the stinging response and the *Ca* worker's cervix

Figure 11. 1. Cork-shaped head adapted in the major workers of *Camponotus impressus* for phragmosis (Magnification 50X).

2. Head of the minor worker of the same (Magnification 100X).

3. Mandibular sensilla of the phragmatic surface. (Magnification 1100X).

1

2

3

received topical venom from the *Lfa* sting. The Co guard immediately retreated inside but was apparently "signalled" to push forward by the major Co workers behind by flexing their gasters. The *Lfa* worker opened its mandibles and grasped those of the venomed guard ant; the pair fell down. A Co major next to the first replaced the guard. The sequence of events was repeated 3-5 times before the *Lfa* replaced the guard in the nest entrance. In 5 cases, 1-7 Co minors escaped the nest during the assaults between the guard and the intruder. Mandibular bites between the *Lfa* guarding the nest entrance and the Co workers inside continued. During the aggression, workers in the brood compartment removed the pupae and older larvae in the lowermost compartment and almost covered the queen with them. Eggs were in the upper compartment. A series of *Lfa* media and minors invaded the Co nest within 55 minutes and killed all the Co majors (13-78) in the colony. The Co minors showed intensive antennal grooming and in a few cases, pulling of the *Lfa* appendages. They were fiercely attacked by more than one *Lfa* and killed. When all the Co workers were killed, the *Lfa* minors started flexing their gaster continuously for 2-7.5 minutes. The response involved no venom secretion and was transmitted to all the *Lfa* workers occupying the Co nest. A similar response was observed when peanut butter was supplied to the *Lfa* workers. One of the gaster-flexing *Lfa* workers ceased the activity, after which all the *Lfa* workers also ceased. Brood transport followed, the *Lfa* workers held the larvae and pupae of the Co in their mandibles and carried them to their nest. The queen showed fast locomotion and biting. She was immediately attacked by 3 *Lfa* minors, stung, and her gaster was severed from her body. The Co colony was used as food by the *Lfa*. The assault was completed within 4.5-5 hours in tube nests

and 6-6.5 hours in natural twig nests, depending on the colony size of *C. impressus*. The escaped Cc workers (7.2-21.5% of the colony) did not enter the nest again (Appendix 4).

Defensive responses:

Alarm and attack responses in Cc were similar to those of the other arboreal ants. Responses A, B, and C were shown by the Cc minor worker when it first confronted the *Lfa* worker outside the nest. Response E was particularly elicited by the guard major Cc workers and was extended by ridding the enemy by throwing it away from the nest before it entered. The alert response, otherwise elicited (D), is carried into the nest from outside by a "messenger" Cc minor which confronted the *Lfa* worker first. Responses J and K were not shown by the Cc workers, and response L was predominantly exhibited by Cc minors. The frequency of the colony responses is tabulated in Table 16.

Camponotus abdominalis floridanus (Buckley)

Habitat:

C. a. floridanus, the Florida carpenter ant, was found epigaeic in the rotting logs and under wilted bark and litter, and hypogaeic adjacent to pieces of wood or a tree trunk. This species was common the the hardwood hammocks, pine woods, and fence rows. Occasionally it nested adjacent to a fire ant mound in the soil. The colony size varied from 300-2400 polymorphic workers; usually a single queen was found. The nest had a single 1.5-2 cm entrance hole.

Colony defense:

Colonies raised in half-rotted wood were exposed to the *Lfa*. The *Lfa* workers reached the *Camponotus abdominalis floridanus* (Caf) nest area

Table 16- Defensive responses shown by *Camponotus impressus* workers during confrontation with *Solenopsis invicta* (5 replications)

Responses	Frequency		Worker caste
	Range	Total	
A	1-2	5	minor
A + B	1-3	9	minor
A + B + C	1-3	9	minor
D	1-6	12	minor & major
E	2-5	13	major
F	9-22	76	minor & major
G	1	2	major
H	1	1	major
I	10-23	72	major & minor
L	2-7	12	minor
Total responses		211	

after 15-20 minutes of exposure. The *Lf* minor worker first moved randomly then oriented to the foraging *Cf* minor and before it antennated the latter, the *Cf* worker retreated, waved its antennae, opened its mandibles, and ran to its nest. The *Lf* laid a trail and recruited majors, minors, and media workers from its nest and moved in a file to the *Cf* nest. Within 3 minutes, the workers from the *Cf* colony emerged, vibrated their bodies, and stayed at one site as a distress signal. They opened their mandibles, secreting mandibular gland secretion and attacked any *Lf* worker reaching near them (0.5-0.2 cm). The mandibular grasps severed the *Lf* heads, antennae, and legs. The *Lf* majors assumed the gaster-flexing position and secreted a venom droplet at their stings. They held their antennae upwards and opened their mandibles. The response elicited alarm frenzy in the surrounding *Lf* minors and media. The second response was mandibular attacks at the legs and antennae of the *Cf* workers, irrespective of their size. Since the *Lf* workers held onto the appendages, the *Cf* workers either severed the *Lf* abdomens or pulled the attacked fore and middle legs through their mandibles. Such *Cf* workers were reattacked by 3-15 *Lf* workers and stung until they died (10-17 min). The *Lf* venom was toxic to the *Cf* when applied topically and subcutaneously.

The mandibular attack was followed by colony agitation in *Cf*, movement of the brood into the deeper tunnels, and secretion of the contents of the mandibular and Dufour's gland. The *Lf* responded by increased gaster-flexing response and slight movement towards the site of stimulation, i.e., the *Cf* nest. The *Lf* workers reduced the gaster-flexing response and entered the outer galleries of the *Cf* nest. The major *Cf* workers guarding the nest entrance emerged from the nest and bit the entering *Lf* worker. However, the *Lf* workers outnumbered the guarding

Caf and invaded the nest. A wave of colony agitation followed in the *Caf* nest, the workers came out holding their immatures in their mandibles, and escaped the nest. The *Lfa* workers were more aggressive, and held onto the escaping *Caf* legs. The stung *Caf* released the brood and exhibited grooming behavior. They rested their gasters on the ground and passed their hind legs through their mandibles. Apparently, this behavior spread the *Lfa* venom to their mouthparts and increased mortality within a short period. The escaping *Caf* workers also curled their gasters under their thorax and squirted the contents of the Dufour's gland via the acidopore to the attacking *Lfa*, no contact between the two species was observed during this response. The *Lfa* exhibited antennal grooming and crippled movement in response to the *Caf* toxin. It became more aggressive and bit the *Caf* workers following them. The *Caf* colony showed a second escape response after 1.2 hours. The *Lfa* workers carried the brood and the dead out of the *Caf* galleries and continued the invasion. The brood was used as food by the *Lfa* but the dead were piled outside the *Caf* nest. The *Caf* queen escaped through a distant hole in the wood with 38 workers and the brood. She was followed by the *Lfa* workers. She opened her mandibles and severed the heads of 3 *Lfa* workers. The surrounding numerous *Lfa* workers crawled on her alitrunk and abdomen, and bit and stung her for 3 minutes. The queen was seen to curl her abdomen and legs and fell on one side within 13 minutes of attack. The escape response was dominant in *Caf*, during 5 experiments, 6.5-47.1% of the colony escaped (Appendix 4). When two thirds of the colony was attacked by the *Lfa* workers, some *Caf* workers showed an ASA response by staying motionless, holding their antennae close to the vertex and running away only when the *Lfa* worker moved away from them. The *Lfa* worker did not

attack the motionless *Caf* worker until it moved. In captivity, the *Caf* workers were eventually attacked by the *Lfa*. The colony was subdued within 8-10 hours. *Caf* workers elicited comparatively fewer spraying responses than the *Formica schaufussi dacsa* workers. In spite of the large-sized *Caf* workers and their strong mandibular grips, the tiny *Lfa* workers attacked and killed the *Caf* workers easily. The *Caf* nest structure did not protect the colony.

The *Caf* colonization near the *Lfa* nest was observed but not understood. The *Caf* workers appeared to be largely scavengers and on a different trophic level than the *Lfa*. They were seen to carry the dead *Lfa* workers from the *Lfa* colony like the *Cyphomyrmex rimosus minutus* workers.

Confrontation Index

In a series of experiments, over 560 *Caf* workers were killed as opposed to 109 of the *Lfa*. The C.I was therefore, 5.1. The concept of numerical confrontation indices in different terrestrial species will be discussed and results summarized in the next section.

CONFRONTATION INDEX

Confrontation studies between colonies of the native ant species and the recently introduced species, *S. invicta*, revealed an aggressive and invasive behavior on the part of the latter. Overt form of aggression is common in Formicidae, and overlapping ecological requirements may induce reciprocal interactions. The laboratory form of interactions can be expected in the field whenever the species compete for nesting sites, territory or food, unless a population equilibrium has been reached (Pontin 1963), or the nature of niches or habitats minimizes contact between the species (Orlan 1965).

The concept of colony interaction was further developed to quantify and compare the total defensive potential of the attacking species. Results of such unitary quantification reflect morphological differences between the species matching the equally diverse variation in their physiological and biochemical processes and thus, their reaction to the defensive secretions. The concept follows as a corollary of the principle used to test biotoxicity of chemicals. The following criteria were considered to develop the unit of aggressiveness:

1. *Solenopsis invicta* was taken as a standard and defensiveness of the native species was measured against it.

2. The defensive secretions secreted by ants are strongly odorous, they are discharged in substantial quantities, and on prolonged exposure, they are fatal to the alien species.

3. Some of the secretions are pheromonic and cause alarm, attack,

attraction and repellence among the workers of the species involved.

4. Satiation and temperature affect aggressive behavior in ants (Wellis 1962)

5. Ants hold such a low aggressive threshold that after detecting their own pheromones, any foreign odor will release attack behavior (Blum 1970, Wilson 1971).

6. There is a rhythmic daily fluctuation in the susceptibility of animals to toxicants.

7. Active principles of arthropod defensive secretions are for the most part, relatively small, highly reactive molecules, potentially capable of interferring with any number of vital chemical processes (Eisner and Meinwald 1966).

8. There is a fluctuation in the diel periodicity of aggression between species

9. Any vibrations of substratum elicit alarm frenzy in ants

10. The colony size of ants varies from less than 100 to several thousand individuals depending on the species.

The technique proposed during confrontation studies is based on the above criteria. The temperature was held constant (27°C) and the ants were obtained from separate colonies, enclosed in individual cells (vide Materials and Methods) for habituation, fed preceding confrontation, and were not fed for 24 hours during confrontation.

Equal numbers of the native species and *S. invicta* determined the comparative dominance of one of them when confronted. Then by using several different multiples of the weaker species against the stronger, a possible "confrontation index" was obtained in relation to *S. invicta*. The numerical values varied from 50 to 5000, depending on the species.

However, the confrontation index (C.I.) was found to be constant for a given species.

By definition,

$$C.I. = \frac{\text{mortality of alien species}}{\text{mortality of } \textit{Lfa}}$$

Let Y = mortality of alien species

and X = mortality of *Lfa*;

then C.I. or A (the constant) = Y/X

or Y = AX

The last equation postulates that there is linear relationship between X and Y. The linearity between the mortality of *Lfa* and the mortality of alien species was verified by the T-Test (Mendenhall 1963), and the value for C.I. could be found by fitting a straight line between the mortality of alien species (Y) and the mortality of *Lfa* (X) by the method of least squares. Derivation of the method of least squares and calculations involved in finding the value of C.I. are given in Appendix 6. The calculated C.I. for each species is shown in Table 17 and Appendix 7, and is graphically presented in Figure 12.

A C.I. greater than 1 denotes the comparatively low defensive potential of those species against the *Lfa*. The superior defensive adaptability of many members of Ponerinae (Odontomachini), Myrmicinae, and Formicinae, establish the independant development of defensive characters that are successful against the *Lfa*. The formicine fauna is not as abundant in Florida as it is in the northern states. The species *L. neoniger* and *Paratrechina* sp. may defend themselves better against the extirpating nature of *Lfa*. The species closely related to the *Lfa*, the native fire ant *S. geminata*, *Pheidole* spp., and *Pogonomyrmex badius* show C.I.'s greater than 1 and are therefore subdued. The dolichoderines and many

Table 17. Results of the confrontation between *Solenopsis invicta* and common terrestrial ant species (24 hr confrontation at 27°C)

Species	Confrontation index (A)
Subfamily: Ponerinae	
Tribe: Ponerini	
Hypoponera opaciceps (Mayr)	7.216
Leptogenys minax Wheeler	14.059
Tribe: Odontomachini	
Odontomachus hyaninodis Wheeler	0.189
Subfamily: Dorylinae	
Tribe: Ecitonini	
Neivamyrmex opacithorax Emery	6.140
Subfamily: Myrmicinae	
Tribe: Myrmicini	
Aphaenogaster texana carolinensis Wheeler	0.436
Aphaenogaster tennesseensis (Mayr)	0.337
Aphaenogaster rahmeadi Emery	0.456
Pheidole dentata Mayr	3.954
Pheidole morrisi Forel	3.978
Solenopsis geminata (Fabricius)	2.102
Pogonomyrmex badius (Latreille)	3.559
Tribe: Attini	
Trachymyrmex septentrionalis (McCook)	15.720

Table 17 Continued

Species	Confrontation Index (A)
Subfamily Dolichoderinae	
Tribe Tapinomini	
Iridomyrmex pruinosum (Roger)	19.639
Conomyrma insana (Buckley)	26.053
Conomyrma flavopecta (M Smith)	9.455
Subfamily Formicinae	
Tribe Formicine	
Lasius neoniger Emery	0.423
Formica schaufussi dolosa Wheeler	2.086
Tribe: Camponotini	
Camponotus abdominalis floridanus (Buckley)	5.309

Figure 12. Confrontation indices of native ant species.

A - *Aphaenogaster texana carolinensis*

Aa- *Aphaenogaster ashmeadi*

At- *Aphaenogaster tennesseensis*

Ca- *Camponotus abdominalis floridanus*

Cf- *Conomyrma flavopecta*

Ci- *Conomyrma insana*

Fs- *Formica schaufussi dolosa*

Ip- *Iridomyrmex pruinosus*

Lm- *Leptogenys manni*

Ln- *Lasius neoniger*

N - *Neivamyrmex opacithorax*

O - *Odontomachus ruginodis*

Pa- *Pogonomyrmex badius*

Pd- *Pheidole dentata*

Pm- *Pheidole morrisi*

Sg- *Solenopsis geminata*

Ts- *Trachymyrmex septentrionalis*

CI- Confrontation index

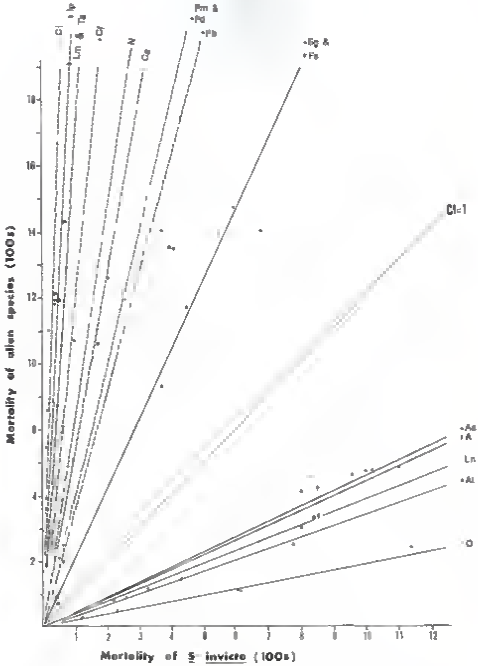


Fig 12 CONFRONTATION INDICES OF NATIVE ANT SPECIES

ponerines had unusually high susceptibility to the *Iſa*. One doryline and one camponotine species follow the same trend. The two closely related dolichoderine species, *Conomyrma insana* and *flavopecta*, reacted very differently when they confronted *Iſa*, the black *insana* was 1.5 times inferior in defense to the yellow *flavopecta*. *C. flavopecta* occurs near the *Iſa* colonies. This species appears to be on a different trophic level from the *Iſa*. The attine species, *Trachymyrmex septentrionalis* showed low initial aggressive frenzy and the primitive *Cyphomyrmex rimosus minutus* was so passive in defense that its C.I. could not be accurately calculated. *C. rimosus minutus* nested near the *Iſa* mounds and collected its dead.

The species that show C.I.'s less than 1 often occupy different habitats than the *Iſa* but their assaults on foraging trails can be expected since they are carniverous, often more so than the *Iſa*. The species of *Pheidole* and *Solenopsis* overlap in their ecological requirements and must adopt some other means of colony protection, like temporal fluctuations in the foraging area, epeasement during frequent encounters, reaching an equilibrium population density after continuous reciprocal interactions, or exhibiting displacement. The species where the C.I. is more than 1 are also either trophically distinct (the fungus growing ants, granivorous harvester ants, saprophegous ants), or trophically very similar. At least one such species, *S. geminata* being the closest in habitat and food requirements to *S. invicta*, indicates displacement (Wilson and Brown 1958).

Only terrestrial ant species were considered for C.I. studies since the arboreal species were far from the *Iſa* in their competition for nesting. The colony confrontations indicate the importance of initial assaults between the guarding ants and the *Iſa* in overcoming their colonies. The colonies were subdued readily once the guards fell.

DISCUSSION AND CONCLUSIONS

From the foregoing studies it is clear that the red imported fire ant, *Solenopsis invicta* Buren, can overcome and destroy, under laboratory conditions, every species of native ants tested. It has been due to more effective aggression on the part of the red imported fire ant, particularly the multifold spectrum myrmicidal activity of its venom and the alarm and trail pheromones which aid fast, aggressive recruitment of its numerically superior worker force. Also of importance are age polyethism, caste polyethism during the attacked and alien brood transport, and effectiveness in nest invasion of the alien species.

As a result of these findings, *Solenopsis invicta* would be expected to outcompete and reduce populations of many of the native species in the field. In fact, frontal assaults between the workers of *S. invicta* and *S. geminata*, *Lasius neoniger*, *Solenopsis xyloni*, *Conomyrma insana*, *C. flavopecta*, *Aphaenogaster tennesseensis*, and even such arboricolous species as *Pseudomyrmex brunneus* and *Camponotus impressus* were observed in different habitats on the Tall Timbers Research Station (see Appendix B). Many of these assaults were observed when the subterranean foraging trails of *S. invicta* crossed the hypogaeic nests of the above species and while tending the same honeydew-producing Homoptera or obtaining nectar from the same flora (e.g. *Campsis radicans*, *Sambucus* spp., *Cephalanthus occidentalis*, *Magnolia* spp., etc.). Aggressiveness of the red imported fire ant did not depend on size, differences in nesting habits, or taxonomic relationship of the ant species within its range. Hamilton (1964),

In discussing the genetical evolution of social behavior, maintained that subspecies will interact fiercely, and species less so. Brian (1965) held the same view, which appears to exclude the behavioral patterns of *S. invicta* and other widely dispersed exodous ants such as *Tetramorium humilis* and *Pheidole megacephala*. Mutual exclusiveness (Haskins and Haskins 1970) and dominance of the last two species over the native ant species is well documented (Haskins 1945, Smith 1936, Wilson and Taylor 1967). The potentially aggressive and accidentally introduced red imported fire ant was found to displace two of its eurytopic congeners, *Solenopsis xyloni* and *Solenopsis geminata*, the former ecologically and the latter ecologically and genetically. The phenomenon has been noted by Wilson and Brown (1958) who found the light form of *S. geminata* disappearing while a dark fer was restricted to the ecotones between wooded areas and open fields. According to Allen et al. (1973), nowhere in Mato Grosso do populations reach the magnitude of *S. invicta* in the United States. *S. invicta* lacks such competition in North America and has dispersed throughout the southeastern United States from Texas to North Carolina and Central Florida since its introduction, nearly 40 years ago. It had probably been established in Alabama for at least 10 years when Dr. W. F. Buren made his first collections in 1945 (Buren 1972). Also, apart from the mammalian toxicity of its nonproteinous venom (MacConnell and Blum 1971, Caro et al. 1957, Favorite 1958, Adroany et al. 1959), introduction of *S. invicta* to North America poses an ecological threat due to its effect on the native fauna. Moreover, no environment on land is more stable than that of the tropics (Darlington 1957, 1959), where this species evolved for its competitive pressures.

From the works of Brian (1955, 1965), Pontin (1961, 1963), Harikovsky

(1963), and Stebayev (1971), in Eurasia, competition between the ant species appears to be a major factor regulating the stability of their population. Individual defense mechanisms, including morphological adaptations and antagonistic allomones, pheromones and kairmones, may decide the defensive potential of the ant species against each other. It is known that the pattern of defensive behavior in ants is the same in a solitary ant or in a group of workers (Wallis 1962, Robertson 1971) and that attack releasing stimuli comes from the alien odor or other threatening situations (Maschwitz 1964, 1966). *S. invicta* was taken as a standard and defensive potential of the native ant species was measured against it by using simple numerical proportions. The "confrontation index" obtained for each terrestrial ant species tended to be relative to its dispersal around the red imported fire ant nest in nature. For example, wherever *Lasius neoniger* population (8000-10,000 nests per acre) approximated the size of those of *S. invicta*, the *S. invicta* nests were sparse. The confrontation index of *L. neoniger* was 0.4, indicating that the defensive potential of a single individual of this species was equivalent to more than two of *S. invicta*. Sparse populations of *S. invicta* were also observed in Introduction Field and Sutty Course, where *S. geminata* populations were high, but they never nested close (distance of 1 meter or less) to each other, and *S. invicta* apparently encroached the habitat suitable to both species. A similar condition commonly occurred in recently cultivated fields, where *S. geminata* nests were common during the first two weeks and then disappeared when *S. invicta* built dominant populations. Both species nest and forage similarly, *i.e.* they overlap ecologically. A dolichoderine species, *Conomyrma insana*, built up high populations and foraged epigeically, unlike *S. invicta*, *S. geminata*,

and *L. neoniger* which foraged partially subterranean up to their prey or honeydew-producing insects. Even though the confrontation index of *C. exsana* with *S. invicta* was 26, the foraging habit along with numerical superiority and repellent allomones, permit high *C. exsana* density in some localized areas (Whitcomb Plots Rep. I, II, Introduction Field, etc.). Some other species such as *Odontomachus ruginodis*, *Aphaenogaster texana carolinensis*, *A. tennesseensis* and *A. rehmandi* had a high confrontation potential, but never built up localized populations and dominated mesophyllic hammocks, habitats *S. invicta* never populated *Pheidole dentata* and *P. moerens*, species nesting in open hardwoods and cultivated fields, foraged solitarily in the nest territory of *S. invicta*, often resorting to differential foraging times and habits and appeasement behavior by exchanging food during their confrontation with the aggressive *S. invicta* workers.

Stebayev (1971) pointed out that the nests of dominant species are spatial organization centers for other ant species which nest around them concentrically and increase their foraging territories radially when the dominant species ceases foraging. The native species of ants would have to resort to a similar distribution if they are ecologically similar to *S. invicta*, i.e., have similar nesting and foraging habits in the presence of *S. invicta*, or they would be displaced. During his study on the competition in British ants, Pontin (1961) opined: "If two different species exploiting an overlapping range of resources (are at the same trophic level) come to overlap in range, then stable competition is, a priori, more likely than displacement, but the only possible equilibrium point may be at too low a density for one of them to maintain itself in the face of other factors, and displacement will follow." Since native species

are limited in their efficiency of exploiting the same resources this would be an obvious cause of such displacement, already observed by Wilson and Brown (1958) and Buren (1972) in the case of *Solenopsis xyloni* and *S. geminata* and many others (Wilson and Oliver 1969, Wilson et al. 1971, Whitcomb et al. 1972).

It was observed that certain species had specialized adaptations which would allow them to coexist with *S. invicta* under field conditions. Examples are *Cyphomyrmex rimosus minutus*, *Conomyrma flavopecta*, *Camponotus abdominalis floridanus* and *Trachymyrmex septentrionalis*. These species were cleptobiotic and possessed specialized morphological and ethological adaptations to escape or tolerate frequent aggressive encounters with the *S. invicta* workers. Interestingly, these species were at a distinctly different trophic level than the red imported fire ant. While alkinetic and aggression suppressing cues (physiological and visual) were remarkably elicited by *C. rimosus minutus* and *T. septentrionalis* (Attini), repellent secretions of *Conomyrma flavopecta* (Dolichoderinae) from the Pavan's gland diminished further attacks by any aggressive *S. invicta* workers. In addition, fast locomotion and nest shifting habits of this species and *Camponotus abdominalis floridanus* (Camponotini) aided their escape and were to the advantage of their necrophoratic nature. A strong digging behavior was induced in the above species and *Pogonomyrmex badius* when their nests were invaded by the red imported fire ant workers, apparently eliminating the source of stimulus by closing the nest holes. Alarm pheromones of *C. flavopecta*, *P. badius*, and *T. septentrionalis* have been chemically identified and the above behavior could be induced (Blum and Warter 1966, McGurk et al. 1966, Crewe and Blum 1972). Legionary ants (Dorylinae) are known for their aggressive, raiding behavior (Schneirla

1957, Rettenmeyer 1963). One common species, *Hexamyrmex spaethonax*, raided *Conomyrma insana* nests successfully, but was killed in large numbers when confronted by the *S. invicta* workers (T.1, 6.1). In nature it raided only weak and partially abandoned red imported fire ant colonies and obtained left over brood either of *S. invicta* or its cleptobiotic species.

It can be conjectured that some species whose range extends from Brazil to the southern United States (*Cyphomyrmex rimosus minutus* and *Trachymyrmex* spp., Weber 1972) are adapted to competing with the red imported fire ant, while many native species are not, in an evolutionary sense. As our knowledge of the evolution of South American ants increases, ethological significance of contest-competition type interactions and related ecodifferentiation of many species will be possible.

The importance of the ethological properties of several alarm pheromones and allesones in defense has been recently established (Wilson and Pavan 1959, Wilson and Bossert 1963, Maschwitz 1964, Eisner and Meinwald 1966, Blum 1969, Moser 1970, Wilson and Regnier 1971, Wilson 1971), and the role of some unidentified trace chemicals has been emphasized (Robertson 1971, Bergstrom and Lofqvist 1973). Since alarm communication and colony defense are combined and in many instances the same substances repel invaders and alert nest-mates, they were referred to as "alarm-defense-systems" by Wilson (1971). Furthermore, alarm response itself is a combination of "alert" (analogous to chemotropotaxis) and "activation" (analogous to ortho- and kinoklinesis). The alarm-defense chemicals have been used to separate species on ethological basis, e.g. *C. insana* from *C. flavopecta*, the sordid brown Florida form of *I. pruinosus* from the reddish northern form (Crewe and Blum 1971). Differences in the behavioral

reactions of these closely related species were obvious when they confronted *S. invicta*.

There is evidence that tactile stimuli such as antennation and stridulation induce alarm and recruitment during assault and prior to escape in Paneinae (*L. minor, O. rugosculis*) and Myrmicinae (*P. badius, S. invicta*). During aggression, different species used their defensive secretions differently. In Dolichoderinae, secretions from the Pavan's gland were directed to the *S. invicta* workers, in Formicinae, Dufour's gland sprays were used, in Myrmicinae, venom was either applied topically (*S. invicta, Aphaenogaster* spp.) or subcutaneously with or without seizing the enemy.

Colony protection was enhanced by species specific nest architecture of terrestrial and arboreal ants. Sometimes nest escape and sequential budding was observed. The arboreal nests of *Pseudomyrmex pallidus*, *P. brunneus*, *Crematogaster atkinsoni*, *C. ashmeadi* and *Camponotus impressus* consisted of several compartments and exit holes which reduced the chance of complete destruction of the colonies and facilitated escape. Many of these species were polygynous and possessed well developed defensive mechanisms. So specialized was the nest guarding behavior of these species that the nest guarding majors of *C. impressus* displayed phragmosis (occluded the nest entrance with their cephalomandibular flattened area) and in Pseudomyrmecinae any intruder was immediately expelled. Insect repellent properties of the secretions from Crematogasterini prevented the nest entry by *S. invicta* workers for several hours. The potency of these alarm-defense chemicals has been tested by Bevan et al. (1961) and Blum et al. (1965). The hypogeaic nest structures of *Hypoponera opaciceps* and *Solenopsis pergandei* had many nest openings close together, or they

were dispersed over a large area as in *Conomyrma insana* and *Iridomyrmex pruinosus* which trailed epigaeically. The nest tunnels were narrow and proliferated so that during nest invasions a part of the colony was protected and colony escape followed (*e.g. P. morrisi* vs. *P. dentata*, *C. insana* vs. *C. flavopecta*, etc.). Many minute species of *Solenopsis* (*Diplorhoptrum*) have been noted for leptobiosis. However, one species discussed here, *S. pergandei*, adopted nocturnal foraging habits.

Mandibular closures are used as a specialized defense mechanism by a generalized ponerine species, *Odontomachus ruginodis*, to attack and to escape, while the well developed sting was hardly used during the aggressive encounters. Antennation and recognition of an alien odor rather than tactile stimulus of its mandibular sensors precede the mandibular snapping mechanism, contrary to what Wheeler (1910) conjectured. Majors of oligomorphic species such as *Pheidole dentata* and *P. morrisi* offered more effective colony defense than the minors (confrontation index of majors was 2.3 and that of oligomorphic populations was 4). However, in a polymorphic species, *Solenopsis geminata*, majors were inferior in defense to minors (confrontation index of polymorphic population was 1.9 and that of the majors alone was 5), as opposed to *S. invicta* where all the population was equally defensive and aggressive. Thus, caste polyethism in colony defense was limited to only some species. More majors were recruited by *S. invicta* while invading the nests of equally defensive species, *S. geminata*, *P. dentata*, *P. morrisi*, *Aphaenogaster texana carolinensis*, *A. tennesseensis*, *A. ashmeadi*, *Lasius neoniger*, *Formica schaufussi detosa*, *Camponotus abdominalis floridanus*, and *O. ruginodis*. Only minors and medie were recruited during the attacks launched on *S. pergandei*, *H. opaciceps* and arboreal species.

Ants are primarily terrestrial and arboreal apterous insects and for the most part are not highly mobile. The detailed information on the defense and escape mechanisms of the native ant species against a comparatively recent introduction has shed light on the defense and aggression of ants in general. Combined with the changes in morphological adaptations, ethological differentiation and degree of social organization in ants lead to differential competitiveness. One species dominates an area and under tenacity of food and nesting sites, other species attain a spatial over dispersion, i.e., spaced so that distances between them are too uniform to have been randomly set. Each species, individually and related species in general, exhibits a high degree of confrontation interactions characterized by passive and active defensive skills, and reduce contest-competition type interactions. Any attempts to manipulate or to replace ant species should not be considered without understanding the interspecific and intraspecific interactions between the species.

APPENDICES

APPENDIX I

Preliminary list of ants of Tall Timbers.

A. Ponerinae

(1) *Euponera gilva* (Roger)

(2) *Hypoponera opacior* (Forel)

(3) *Hypoponera opaciceps* (Mayr)

(4) *Odontomachus ruginodis* Wheeler

(5) *Amblyopone pallipes* (Haldeman)

(6) *Leptogenys manni* Wheeler

B. Dorylinae

(1) *Neivamyrmex texana* Watkins

(2) *Neivamyrmex opacithorax* (Emery)

(3) *Neivamyrmex* sp.

(4) *Neivamyrmex* sp

C. Pseudomyrmidae

(1) *Pseudomyrmex brunnea* F. Smith

(2) *Pseudomyrmex pallidus* F. Smith

D. Myrmicinae

(1) *Pogonomyrmex badius* (Latreille)

(2) *Aphaenogaster ashmeadi* Emery

(3) *Aphaenogaster fleminga* M. R. Smith

(4) *Aphaenogaster fulva* Roger

(5) *Aphaenogaster mariana* Wheeler

(6) *Aphaenogaster texana* Emery

(7) *Aphaenogaster floridana* M. R. Smith

(8) *Aphaenogaster tennesseensis* (Mayr)

(9) *Pheidole bicarinata vinelandica* Forel

(10) *Pheidole dentata* Mayr

(11) *Pheidole floridana* Emery

(12) *Pheidole metallescens* Emery

(13) *Pheidole morrisi* Forel

(14) *Pheidole* sp.

(15) *Cardiocondyla emeryi* Forel

(16) *Cardiocondyla nuda minutior* Forel

(17) *Cardiocondyla wroughtoni bimaculata* Wheeler

(18) *Crematogaster minutissima* Mayr

(19) *Crematogaster* sp.

(20) *Crematogaster ashmeadi* Mayr

(21) *Crematogaster clara* Mayr

(22) *Crematogaster atkinsoni* Wheeler

(23) *Crematogaster vermiculata* Emery

(24) *Crematogaster lineolata* (Say)

(25) *Crematogaster punctulata* Emery

(26) *Monomorium viridum* Brown

(27) *Monomorium pharaonis* (Linne)

(28) *Solenopsis geminata* (Fabricius)

(29) *Solenopsis invicta* Buren

(30) *Solenopsis* sp.

(31) *Solenopsis* sp.

(32) *Solenopsis pergandei* Forel

(33) *Solenopsis picta* Emery

(34) *Wasmannia americana* Emery

(35) *Macromischa floridanus* Wheeler

(36) *Leptothorax curvispinosus* Mayr

(37) *Leptothorax schaum.* Roger

(38) *Wasmannia auropunctata* (Roger)

(39) *Strumigenys louisianae* Roger

(40) *Smithistruma rastrata* (Emery)

(41) *Smithistruma* sp

(42) *Cyphomyrmex rimosus minutus* Mayr

(43) *Trachymyrmex septentrionalis* (McCook)

E. Dolichoderinae

(1) *Dolichoderus pustulatus* Mayr

(2) *Tridemyrmex pruinosus* (Roger)

(3) *Conomyrma insana* (Buckley)

(4) *Conomyrma flavopecta* M. R. Smith

(5) *Tapinoma sessile* (Say)

F. Formicinae

(1) *Brachymyrmex depilis* Emery

(2) *Brachymyrmex obscurior* Forel

(3) *Camponotus pennsylvanicus* (DeGeer)

(4) *Camponotus americanus* Mayr

(5) *Camponotus castaneus* (Latreille)

(6) *Camponotus carye discolor* (Buckley)

(7) *Camponotus socius* Roger

(8) *Camponotus abdominalis floridanus* (Buckley)

(9) *Camponotus nearticus* Emery

(10) *Camponotus impressus* (Roger)

(11) *Paratrechina longicornis* Latreille

(12) *Paratrechina* sp.

(13) *Paratrechina* sp.

(14) *Prenolepis imparis* (Say)

(15) *Lasius neoniger* Emery

(16) *Formica archboldi* M. R. Smith

(17) *Formica schaufussi dolosa* Wheeler

(18) *Formica pallidefulva* Latreille

APPENDIX 2

Analysis of variance: Frequency of mandibular closures exhibited by *O. rugosus* in the presence of dental stick and *S. invicta* workers.

Source	df	SS	MSS	F
Treatment	11	63.43	5.76	21.40
Error	108	29.10	0.27	
Total	119	92.53		

APPENDIX 3

Duncan's new multiple-range test showing the effect of presence and absence of antennal flagella on the mandibular closures in *O. augustula*. (Transformation = square root X + 0.01)

a	b	c	d	e	f	g	h	i	j	k	l
2.64	2.36	2.33	1.93	1.86	1.64	1.61	1.55	1.47	1.16	0.28	0.19

a to e: ants in the presence of *S. invicta* workers.

f to j: ants in the presence of dental stick.

k and l: ants without antennae and in the presence of *S. invicta* and dental stick respectively.

e and f: whole ants

b and i: all hairs removed

c and h: with only left flagella

d and g: with only right flagella

e and j: flagella coated with paraffin wax

APPENDIX 4

Escape responses of arboreal species during their nest invasion by *S. invicta* (n = 5).

Species	Percent Colony Escape		
	Range	Mean	S.D.
Crematogaster atkinsoni	16.1-62-3	35.78	22.00
Crematogaster ashmeadi	10.8-29.7	20.46	6.88
Crematogaster minutissima	36.01-42.69	39.45	3.20
Pseudomyrmex pallidus	2.50-29.79	14.06	11.70
Pseudomyrmex brunneus	5.76-23.21	10.43	8.19
Camponotus [Colobopsis] impressus	7.24-21.50	12.38	5.53
Camponotus abdominalis floridanus	3.96-45.13	21.01	16.31

F for *Crematogaster atkinsoni* and *Crematogaster ashmeadi*, *Pseudomyrmex pallidus* and *Pseudomyrmex brunneus*, and *Camponotus [Colobopsis] impressus* and *Camponotus abdominalis floridanus* not significant.

APPENDIX 5

Differential nesting of *Pseudomyrmex pallidus* in vertical and horizontal *Catalpa speciosa* twigs (n = 23).

Vertical twigs			Horizontal twigs		
Range	%	Mean	Range	%	Mean
9-97	87 43	39 30	0-3	4.52	0.43

Student - t, significant (P = 0.001).

APPENDIX 6

Derivation of least square for the confrontation index

The linear relationship between the mortalities of the alien species (Y) and *S. invicta* (X) is represented in Fig. 12. The mortalities of confronting species were interdependent and no mortality was observed in the absence of any one of the two. Therefore, the intercept of the straight line, representing the constant "A" or C.I., should have zero value. The constant for the intercept was hence disregarded (see Mendenhall 1963).

Thus, the equation can be written as:

$$Y = AX \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots \quad (1)$$

The constant A, should have a value such that the sum of the square of error (or ΣE^2) is least,

$$\text{or} \quad \frac{d(\Sigma E^2)}{d\,A} = 0$$

The error between the computed value of Y and the observed value of Y, from the first equation:

$$E = Y - AX$$

$$A = \Sigma XY/\Sigma X^2 \qquad \text{where } A = \text{C.I. or confrontation index}$$

APPENDIX 7

Results of confrontations of common terrestrial ant species towards *S. invicta* (24 hr confrontation at 27°C, n = 5).

Species	Mortality		Confrontation Index
	S. invicta (X)	alien (Y)	
PONERINAE			
Hypoponera opaciceps	30	240	7.216
	32	275	
	30	216	
	43	276	
	40	273	
Leptogenys maxi	20	238	14.059
	11	204	
	11	246	
	12	260	
	23	246	
Odontomachus ruginodis	122	27	0.189
	229	48	
	613	107	
	606	113	
	1238	238	
DORYLINAE			
Neivamyrmex opacithorax	80	489	6.140
	78	473	
	73	492	
	89	483	
	63	436	
MYRMICINAE			
Aphaenogaster texana carolinensis	850	336	0.436
	843	332	
	804	306	
	800	411	
	853	426	

Species	Mortality		Confrontation Index
	Life (X)	Alien (Y)	
Aphaenogaster tennesseensis	785	261	0.337
	438	145	
	324	119	
	264	89	
	226	78	
Aphaenogaster wheeleri	961	460	0.456
	1022	471	
	836	453	
	1238	479	
	1006	476	
Pheidole dentata	502	1148	3.954
	168	859	
	843	4254	
	210	1065	
	505	1146	
Pheidole morrisi	256	927	3.978
	240	960	
	259	994	
	202	907	
	226	946	
Solenopsis geminata	1110	2795	2.102
	2305	4680	
	600	1273	
	556	1187	
	670	1203	
Paganomyrmex badius	62	245	3.559
	373	1200	
	540	2006	
	53	213	
	58	199	
Trachymyrmex septentrionalis	11	158	15.720
	20	320	
	11	160	
	10	160	
	9	160	

Species	Mortality		Confrontation Index
	ants (X)	alien (Y)	
DOLICHODERINAE			
Iridomyrmex pruinosus	76	1229	19.639
	38	1005	
	45	1000	
	65	970	
	78	1821	
Camponotus lasius (black form)	33	906	26.053
	12	546	
	17	657	
	40	582	
	43	951	
Camponotus flavopecta	46	543	9.855
	34	248	
	60	594	
	52	870	
	58	607	
FORMICINAE			
Lasius neoniger	48	23	0.423
	62	26	
	68	31	
	62	23	
	73	30	
Formica schaufussi dakota	372	726	2.086
	445	570	
	40	72	
	41	89	
	38	92	
Camponotus abdominalis floridanus	109	564	5.309
	63	349	
	62	352	
	72	380	
	76	396	

APPENDIX 8

Interspecific confrontations between *Solenopsis invicta* and native species observed on Tall Timbers area during 1969-72.

Species	Location	Date
Pseudomyrmex brunneus	Hall Island	May 16, 1971
Aphaenogaster texana	Sheep Island	May 27, 1972
Aphaenogaster tennesseensis	Hall Island	May 27, 1972
Solenopsis geminata	Introduction Field	June 3, 1970
		May 19, 1972
Solenopsis pergandei	Whitcomb Plots	September 3, 1970
	Rep. II	
Conomyrma flavopecta	Anders Course	September 17, 1971
Conomyrma insana	Whitcomb Plots	July 10, 1972
	Rep. I	
Camponotus abdominalis floridanus	Vickers Field	August 10, 1970
		May 3, 1972
Lasius neoniger	Beadle Course	November 25, 1969
	Tripsacum Course	May 7, 1971

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I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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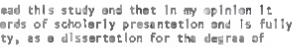

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This dissertation was submitted to the Dean of the College of Agriculture and to the Graduate Council, and was accepted as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

August, 1973

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